ADAPTATION OF WHEAT TO A TROPICAL ENVIRONMENT

Akhmad Zubaidi

Sarjana Pertanian, Agronomi (Mataram)

MScAgric (Adel)

Thesis submitted for the degree

of

Doctor of Philosophy

School of Agriculture, Food and Wine

The University of Adelaide

September 2015

TABLE OF CONTENTS

LIST OF TABLES

LIST OF SUPPLEMENTARY TABLES

LIST OF FIGURES

LIST OF SUPPLEMENTARY FIGURES

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

I give consent to this copy of my thesis, when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968.

I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time

Akhmad Zubaidi

Acknowledgement

I would like to express my sincere gratitude and appreciation to my supervisors, Associate Professor Glenn K. McDonald and Associate Professor Gurjeet Gill. I owe the most gratitude to Associate Professor McDonald, who has given generously of his time and provided excellent supervision throughout my study, especially for his endless patience, understanding and invaluably constructive criticism. I am sincerely thankful to Associate Professor Gill for his invaluable guidance, friendly advice and constructive criticism during the project work and writing. I would also like to sincerely thank my external supervisor, Prof. Mansur Ma'shum from the University of Mataram for his guidance and encouragement during my study, especially field work on Lombok Island Indonesia.

I gratefully acknowledge and thank to all staff and friends of the School of Agriculture, Food and Wine, especially the Agronomy Lab, Waite Institute for their help and friendship. My thanks to Ms. Teresa Fowles for her help in ICP analysis. My special thanks to Dr. Ian Dundas for his help and frienship during my time in Adelaide.

I express my thanks to the Directorate General of Higher Education (DIKTI), Indonesian Department of Education for granting me a scholarship and to the Rector of Mataram University for giving me study leave for conducting this study. My warm thanks also for Dr. Budi Indarsih, Coordinator of DIKTI scholarship at University of Mataram, for her support and guidance on arganising my scholarship.

I also wish to express my sincere gratitude to my wife, Ratna, and my children, Annisa, Amalia and Arief for their endless support and patience in every situation. My special thanks also to all my brothers and sisters for their help and moral support during my field experiments in Lombok.

ABSTRACT

Wheat consumption in Indonesia is continuously increasing. Indonesia imports considerable amounts of wheat for domestic consumption and processing and this has increased with economic development. Therefore to lower the high import of wheat grains, Indonesia should have domestic production. Even though Indonesia straddles the equator, the high altitudes in many parts of Indonesia means that wheat could potentially be grown during the dry season as it is more drought tolerant than rice. However, improved adaptation of wheat to tropical environments is needed to achieve this goal.

Lombok Island (8.5°S 116°E) is suggested to be one of the potential areas of wheat growing. The average maximum temperature at the capital city, Mataram (low altitude) is 30-32°C during day time and minimum at 20-23°C at night but this is moderated by elevation in the centre of the island. The lowest temperature during the year is between June and August which also is the dry season. Lombok's current farming system consists of two rice plantings during the rainy season and a non-rice planting during the dry season. May to September is proposed to be the wheat growing period on Lombok to have the plant flowering during the time of lowest temperatures and coincidently with no or limited rainfall during grain development to avoid grain sprouting in the field before harvested.

In order to investigate the adaptation of wheat on Lombok Island Indonesia, a series of growth chamber and field experiments was conducted. The initial controlled environment experiments at Adelaide University that examined patterns of apical development and seedling growth were done at a continuously high temperature (32/23°C) day/night to imitate temperatures at lowland sites of Lombok Island while in later experiments in which development, growth and yield were studied, the temperature treatments were expanded to 3 temperature regime, 32/23°C, 28/20°C to imitate lowland and highland temperatures of Lombok Island and 25/15°C to represent a temperature more typical of a wheat producing area in a temperate environment. Field experiments were done in two consecutive years 2010 and 2011 at 3 different elevation sites on Lombok Island-Indonesia: Sembalun (1000masl), Narmada (200 masl) and Gunung Sari (10masl) in 2010, and Sembalun, Senaru (500masl) and Lekok (10masl) in 2011. Seeds were sown at 6 sowing times in 2010 and 3 sowing times in 2011. A range of Australian varieties with different maturities were grown and later two Indonesian varieties were included.

Plant development was rapid under continuously high temperature environment both under controlled environment experiments and in field experiments with double ridge occurring 15-30 days after sowing and flowering occurring 40-70 days after sowing in most varieties. There was good correlation in the rates of development under controlled environment and field conditions. The differences in flowering time were related to photoperiod sensitivity and intrinsic earliness among varieties. The results suggested that early maturing varieties (eg. Axe) developed very rapidly which may limit their yield potential.

In the field trials on Lombok, wheat productivity was influenced by elevation and sowing date. At lowland sites yields were about 1 t/ha or less, whereas when grown at 500 masl elevation or above yields were substantially higher and ranged from 2.2-3.2 t/ha. The change in yields with elevations was associated with changes in mean temperature: the change in yield with increasing temperature was -55 $g/m^2/°C$. The optimum sowing time at higher elevation on Lombok was from mid-May to early June which allowed plants to flower in the cooler and drier time of the year, and this also allow wheat to fit in with the current cropping systems. Mid-season varieties that flowered after 65 days were generally higher yielding than earlier flowering or later flowering varieties. Yield was most strongly related to grains/m^2 which emphasised the importance of the timing of the phase of ear and floret development for sink development in this short season environment.

Growing wheat at 32/23°C greatly reduced wheat yields compared to 28/20°C and 25/15°C due to much more rapid development, lower net photosynthesis rates and lower accumulation of water soluble carbohydrates (WSC). This resulted in reduction in both grain number and kernel weight with yield being relatively more affected by changes in grain number. There was some evidence of genetic variability to heat stress. The differences in yield among varieties was related to differences in photosynthetic rate, stomatal conductance as well as the amount and remobilisation of WSC. Two Indonesian varieties were more tolerant to high temperature than Australian varieties.

The results of this work suggested that it is feasible to grow wheat on Lombok Island at elevations above 500 m. Mid-season varieties that flower after 60-70 days appear to be the most promising pattern of development. There appears to be significant genetic variation in yield to allow further development of improved varieties. Future work should consider adapting wheat into broader potential areas of Indonesia, developing appropriate cropping practices for different altitude and yield potential areas, and introducing or breeding new heat stress tolerant varieties.

CHAPTER 1

INTRODUCTION

Wheat is one of world's major sources of dietary calories and proteins. It is a temperate cereal that is grown over a wide range of precipitation and temperature conditions, mostly in the range from 25° to 50°latitude; however, wheat production has expanded into tropical and subtropical areas to less than 15° latitude. This has been due in part to the availability of more widely adapted semi-dwarf germplasm (Music and Porter, 1990; Badaruddin et al., 1999)as well as the growing demand for wheat-based products in these regions. In these tropical and subtropical environments, wheat is grown during the cool season and often at high altitude to minimise the adverse effects of high temperature.

Wheat has been the most traded agricultural product since the 1960s. World imports of wheat have increased from 40 Mt in the 1960s to almost 144 Mt in 2010 (FAO, 2012). Tropical countries in South East Asia, including Indonesia, import considerable amounts of wheat for their domestic consumption and processing and this has increased considerably with economic development. South East Asian countries imported about 1 Mt of wheat grain in the 1960s which increased to 11.9 Mt in 2010. Indonesia imported almost 5 Mt of wheat grain from producer countries such as Australia, Canada, United States and others in 2010 to the value of $US 1.424 million (FAO, 2012)

Current consumption of wheat in Indonesia is 21.5 kg/person/year. This is lower than average world consumption (65.9 kg/person/year) but it is steadily increasing (FAO, 2012). Increased production of wheat in Indonesia would help to lower the high cost of imported wheat grains. Consequently, the Indonesia Department of Agriculture aimed for some commercial production of wheat by 2014 (Suhendra, 2012). Potentially, wheat could grow during the dry season as it is more drought tolerant than rice. However, improved adaptation of wheat to tropical environments is needed to achieve this goal.

Improvement in the adaptation of wheat to tropical environments is needed to increase local production of wheat in Indonesia. Wheat is a winter cereal that evolved in temperate environments and tropical conditions are not favourable for wheat growing and production. Among abiotic stresses, heat and drought stress and a number of nutritional disorders are important factors limiting wheat production in the tropics (Muzilli, 1984; Fischer, 1985; Kohli and McMahon, 1988). Also, when grown in the warm tropics; wheat develops rapidly which shortens the growing period and leads to reduced growth and yield (Fischer, 1985; Rawson, 1988). Wheat grown in the tropics may establish poorly (Fischer, 1985) and vegetative development can be rapid leading to low grain number and individual grain weight (Bagga and Rawson, 1977; Warrington et al., 1977; Midmore et al., 1982; Fischer, 1985). High temperatures during grain development also could reduce the quality of flour dough(Wardlaw, 2002). If the time from seedling to flowering could be made longer, wheat could potentially have a higher biomass production as well as higher harvest index and consequently greater yield (Fischer, 1985). This requires an understanding of phenology in the target environment to find varieties best adapted to tropical conditions.

While not the focus of the present study, another problem of wheat growing in tropics and subtropics is nutritional disorders. Tropical and subtropical soils are often deficient in phosphorus and micronutrients such as boron and zinc and toxicity in aluminium is common. At the same time, the high humidity of the tropics together with the high temperature increase the incidence of pests and diseases (Wall, 1987).

In summary, these tropical conditions lead to: (a) poor crop establishment, (b) accelerated growth and development processes, (c) reduced grain number and weight leading to low yields, and (d) lower grain quality and dough characteristics.

Previous research on wheat responses to high temperatures has frequently examined effects at specific growth stages, such as heat stress during grain filling or at flowering. However, there is little information about plant growth and development in a continuous high temperature typical of that experienced in tropical environments. The aim of this project is to define wheat characteristics that can reduce the limitation of wheat production in the tropics with Lombok Island, Indonesia as the target area. In order to achieve the aim, three objectives have been set up, which are (1) to define the optimum pattern of development for wheat in high temperature (30°C/23°C day/night temperatures), (2) to define the optimum time of sowing and flowering for wheat in Lombok to gain a reasonable yield, (3) to examine the effects of high temperature stress and maturity type on yield and yield components. The information from this project will help in developing cropping system and requirements for adaptation and production of wheat in the tropics.

REFERENCES

Badaruddin, M., Reynolds, M.P., Ageeb, O.A.A., 1999. Wheat management in warm environments: effect of organic and inorganic fertilizers, irrigation frequency, and mulching. Agronomy Journal 91, 975-983.

Bagga, A.K., Rawson, H.M., 1977. Contrasting responses of morphologically similar wheat cultivars to temperatures appropriate to warm temperature climates with hot summers: a study in controlled environment. Australian Journal of Plant Physiology 4, 877-887.

FAO, 2012. FAO Statistics (http://www.fao.org/crop/statistics/en/). Food and Agriculture Organisation of The United Nations, Rome, Italy.

Fischer, R.A., 1985. Physiological limitations to producing wheat in semitropical and tropical environments and possible selection criteria. Wheats for more tropical environments. A proceedings of an international symposium on wheat production and research in tropical environments, held in Mexico on 24-28 September, 1984. CIMMYT, Mexico, pp. 209-230.

Kohli, M.M., McMahon, M., 1988. A prospective of research need for non irrigated tropical condition. In: Klatt, A.R. (Ed.), Wheat production constrains in tropical environments. CIMMYT, Mexico.

Midmore, D.J., Cartwright, P.M., Fischer, R.A., 1982. Wheat in tropical environments. I. Phasic development and spike size. Field Crops Research 5, 185-200.

Music, Porter, 1990. Wheat. In: Stewart, B.A., Nielson, D.R. (Eds.), Irrigation of Agricultural Crops. ASA - CSA - CSSA, Madison - Wisconsin.

Muzilli, O., 1984. Soil management as alternative for minimizing environmental constraints for wheat production in the semi tropical areas of Brazil. In: Villareal, R., Klatt, A.R. (Eds.), Wheat for more tropical environments. CIMMYT, Mexico, pp. 231-238.

Rawson, H.M., 1988. Effects of high temperatures on the development and yield of wheat and practices to reduce deleterious effects. In: Klatt, A.R. (Ed.), Wheat production constraints in tropical environments. Proceedings of the international conference, Chiang Mai, Thailand, 19-23 January 1987., pp. 44-62.

Suhendra, 2012. Kurangi Impor, RI Produksi Gandum Secara Massal Mulai 2014. Detik Finance. Detikcom, Jakarta.

Wall, P.C., 1987. Central and South America. In: Klatt, A.R. (Ed.), Wheat production constraints in tropical environments. CIMMYT, Mexico, pp. 27-36.

Wardlaw, I.F., 2002. Interaction between drought and chronic high temperature during kernel filling in wheat in a controlled environment. Annals of Botany 90, 469-476.

Warrington, I.J., Dunstone, R.L., Green, L.M., 1977. Temperature effects at three development stages on the yield of the wheat ear. Australian Journal of Agricultural Research 28, 11-27.

CHAPTER 2

REVIEW OF LITERATURE

1. WHEAT PRODUCTION IN INDONESIA

Early efforts to improve adaptation of wheat to higher temperature environments of the tropics began in the late 1970s. Wheat production trials in tropical countries have been run since 1978 by CIMMYT. Two consecutive international conferences were held by CIMMYT in 1984 and 1987 addressing the problems related to adapting wheat to warmer tropical environment (Villareal and Klatt, 1985; Klatt, 1988). The conferences emphasized that high temperature is not the only major problem of wheat production in the tropics but also adequate water and nutrient availability are needed to support the fast-growing plants.

In Indonesia, wheat has been cultivated since the 1900s by the Dutch and Portuguese administrations to fulfil the needs of the Europeans living in the islands. Trials were conducted in western Java, northern Sumatra, and Timor. However, there was no further work on wheat production in Indonesia after the Europeans left in the 1940s until recent times when the issue of greater domestic production started to receive attention.

Recent research efforts began in the 1980s with the introduction of Indian and Pakistani wheats cultivars. Farmer trials in 2000 in Central Java highland yielded 4 to 5 t/ha grains. A study in different places with different altitudes showed yields varied between 1.8 t/ha in the lowland to 5.8 t/ha in the highest altitude, suggesting that elevation through its effect on temperature plays an important role in Indonesian wheat production (Handoko, 2007). However, the trials have only been done for a single genotype (DWR 162) introduced from India, and only on Java Island. Other work suggests that yields on Lombok may be lower. Gusmayanti *et al.* (2006) modelled wheat production on Lombok Island using Compromise Programming based on potential productivity and growing time.

The modelling predicted that wheat grain yields in Lombok to be 1.5-3.0 t/ha. These data suggest that constraints for wheat growing on Lombok maybe greater than in other parts of Indonesia. Even though the economic value of wheat is less than rice, wheat production is still profitable in Lombok because wheat is relatively more tolerant to dry environments compared to rice. The previous work also indicated that the highland of the northern part of Lombok Island is the most suitable area for wheat production (Gusmayanti et al., 2006). However, there is no experimental work to validate the prediction and to determine wheat adaptation more general.

This Review of Literature will examine the factors that will influence the adaptation and yield and wheat to tropical environments. While it is recognised that there are range of biotic and abiotic factors that will determine the yield and quality of wheat in the tropics, the review will focus on the importance of high temperature.

2 THE ENVIRONMENT OF LOMBOK

Location

The Indonesian island of Lombok (8.5°S 116°E) belongs to the province of West Nusa Tenggara and is a part of the Nusa Tenggara Islands (Lesser Sunda Islands). Lombok is located east of Bali Islandand is separated from Bali by the Lombok Strait. Lombok is almost circular in shape with Mataram as the capital and largest city. The strato-volcano Mount Rinjani soaring up to a height more than 3700 m determines the topographical form of Lombok. Lombok topography shows a slope from north to south with Rinjani the highest point, the middle part spreads from west to east as the lowland, while the south of the island forms a hilly landscape (Figure 2.1).

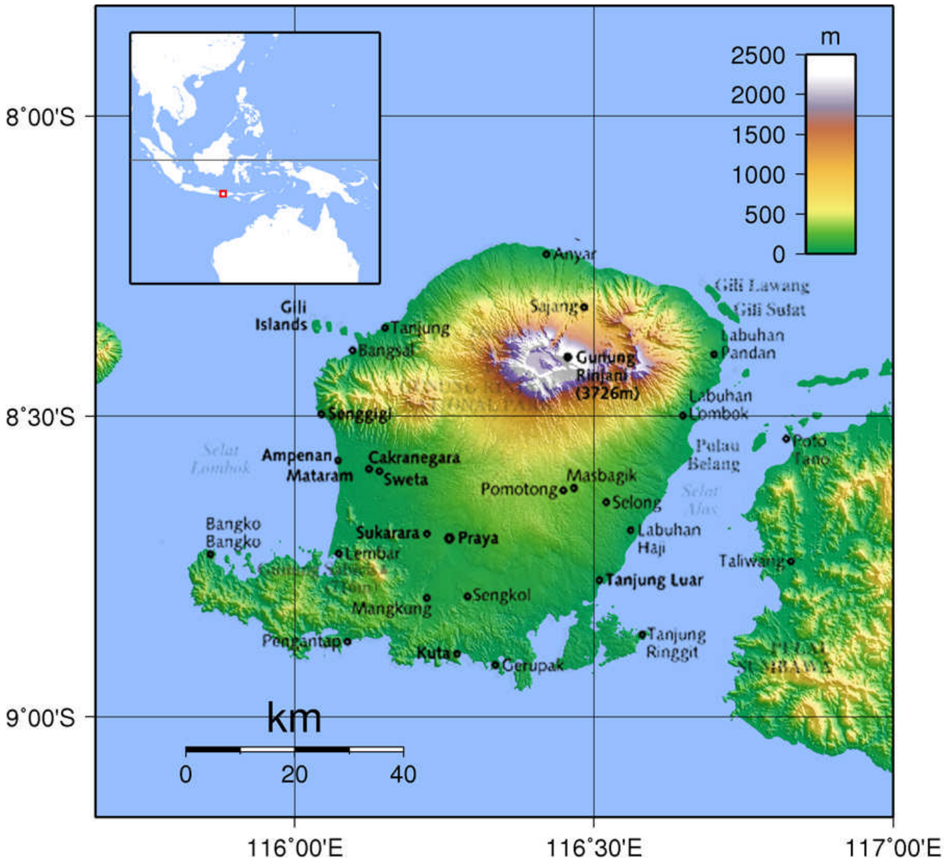


Figure 2.1: Map of Lombok Island with different altitude; the highest altitude around Mt Rinjani / Segara Anak Lake (>3000 m). (http://commons.wikimedia.org/wiki/user:SadalMelik#islands)

Weather

Lombok is located near the equator (around 320 km to the south) and has a hot and humid environment. Being so close to the equator means that daylength on Lombok is constantly 12 hours year round and temperatures are also relatively constant. The average maximum temperature at the capital city, Mataram (low altitude), is 30-32°C during day time and minimum at 20-23°C at night. Lombok has 2 seasons, which are the wet season from October to March while the months of May to September are the dry season (WMO, 2012). There is no or very little rain during these dry months (Figure 2.2). The wettest area is in the highland of Mt. Rinjani, which also has the lowest temperatures on the island.

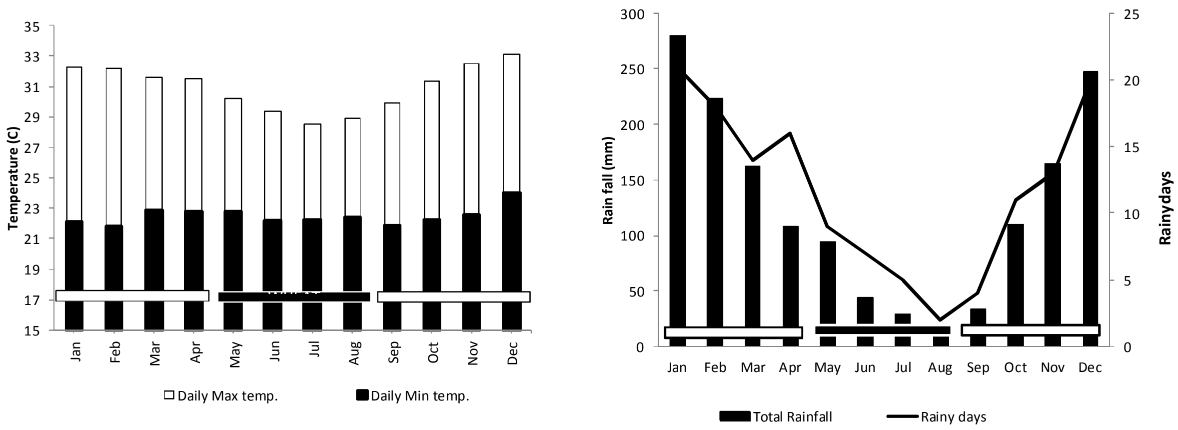


Figure 2.2: Average daily maximum and minimum temperature of Lombok Island (left) and rainfall and rainy days (right). The horizontal bars shows 3 cropping patterns on Lombok; white bars for rice and black for other crops and proposed for wheat (WMO, 2012)

Based on the maximum temperatures on Lombok, wheat could be grown since it can tolerate maximum temperatures of 35°C even if it exceeds the optimum temperature of 20-25°C (Porter and Gawith, 1999). Wheat may be grown during May to August when the lowest maximum daily temperature is about 30°C (Fig. 2.2). This may not have a marked negative effect on spikelet formation because at that time the temperature is only slightly higher than maximum temperature for spikelet formations reported for wheat (25°C) (Porter and Gawith, 1999). Wahid et al. (2007) suggested that the mean daily temperature should not exceed maximum temperature requirement by more than 15°C. Therefore, theoretically the mean daily temperatures on Lombok, while high, are still suitable for wheat when sown in April/May. The moderating effect of altitude on temperature will also mean there is potential for wheat production in the highland areas.

Soil properties

During the last 3 decades, farmers in Lombok have used high inputs of phosphorus and potassium in their farming practices. This intensive application of fertiliser caused a build up of total phosphorus and potassium in the soil. A potential effect of this is that it may suppress the availability of micronutrients especially zinc (Robson and Pitman, 1983; Sofyan et al., 2004). A survey of soils on Lombok found that 90% of the area has a high phosphorus level and only 9.8% has medium content of phosphorus (Table 2.1). In contrast, all of Lombok's soil has low zinc concentration, with 56% having a soil Zn concentration of 1-2 mg/kg and the other 44% with less than 1 mg/kg (Sofyan et al., 2004). Organic carbon concentrations in Lombok's soils are generally low, with 34% having levels less than 1% (Table 2.1).

Table 2.1: Nutrition content of Lombok's soil(Sofyan et al., 2004)

	Low	Medium	High	No. samples/ area covered
C organic	34.2%	63.0%	2.8%	319 samples
Phosphorus	0	9.8%	90.2%	123,000 ha
Potassium	0	0	100%	123,000 ha
Zinc	43.8%	56.2%	0	122,655 ha

Wheat growing in the existing farming system

Lombok's current farming system consists of two rice plantings during the rainy season and a non-rice planting during the dry season. The first rice planting starts in September/October when the rainy season begins, followed by a second rice planting season in January/February. The third planting, which occurs during the dry season, starts in May/June, at the end of the rainy season or at the beginning of the dry season. The dry season crops are mainly soybean and peanuts and sometimes corn. These crops rely on the residual moisture from the rice crop because of the low rainfall received during this period.

Wheat may be suitable as a crop after the second rice crop for 3 reasons: (a) wheat will not replace rice which has a high preference among Lombok farmers (Gusmayanti et al., 2006), (b) wheat planting during this season coincides with the lowest temperature of the year round, and (3) it also coincides with the dry season at the end of the growing period. This dry condition has advantages for utilizing relatively limited amounts of soil water while rice cannot use it, avoiding high occurrence of pest and diseases, and avoiding risk of sprouting of grain before harvest.

Integrating wheat with rice cropping is not a new system. Rice-Wheat Cropping Systems (RWS) have been practised for a long time in Asia. In China, it has been practised since the year 700 while in South Asia it has been recorded since 1872 (Gupta et al., 2004). Wheat is produced during the cold winter period when conditions are less suitable for other crops. However, researchers are now questioning the sustainability of this system in South Asia because of continuous decline of their production. The most commonly-cited reason for the decline is low organic matter and nutrient contents of the soils. Incorporating plant residues to the soil is rarely done partly because of limitation of turnaround time between crops (Khybri et al., 1992; Prasad et al., 1999; Chettri et al., 2003; Gupta et al., 2004).

In some tropical countries such as those in South Asia (India, Pakistan and Bangladesh), wheat is commonly sown when the temperature is still quite high, but most of its growing periods is on their so-called ‘winter time’, when the temperature is relatively low. The proposed Rice Wheat System (RWS) in Lombok, however, will not be completely similar with that practised in South Asia since Lombok has no winter season as the temperatures are relatively constant all year. Sowing wheat at the right time on the right part of Lombok Island could help the development of a wheat production system on

Lombok. Long term practices of rice-wheat system, as well as existing rice system in Lombok could face the similar nutritional problems as those experienced in other parts of South Asia, since Lombok's soils also have a low content of organic matter and there are some limitations of soil fertility (Sofyan et al., 2004). Other efforts to enrich soil organic matter have to be done in order to maintain the sustainability of Lombok farming practises.

3 WHEAT GROWTH AND DEVELOPMENT

Growth is a quantitative process measured as an increase in size, while development is a qualitative change in form. In general, phasic development (the development through well-defined stages of growth) can be considered as chronological development of wheat plant from germination to maturity. The pattern of wheat development plays a critical role in determination of yield, by its direct effect on yield components and indirect effects through the timing of developmental stages in relation to environmental changes. It is greatly modified by environmental factors such as temperature, drought, nutrition and their interactions with cultivar sensitivity to these factors. The correct timing of phasic events is generally considered the most important factor for wheat adaptation and maximum yield in various environments (Acevedo et al., 2002). The severity of the yield depression depends on the developmental stage at which the stresses occur (Acevedo et al., 1991).

Various stages of wheat development are usually distinguished: germination, emergence, tillering, double ridge, terminal spikelet, first node or beginning of stem elongation, boot, spike emergence, anthesis and maturity. These stages are generally grouped into four phases of development: germination to emergence; emergence to double ridge, double ridge to anthesis, and anthesis to maturity. Physiological maturity is when the grain growth is completed and the grain starts to dehydrate. Visually, it is defined as the time when the flag leaf and spikes turn yellow (Acevedo et al., 2002).

Germination to emergence

A wheat seed begins germination by absorbing water. Adequate soil moisture and temperature and supply of oxygen are needed for this to occur. The speed of germination is driven largely by temperature and starts to decrease above 32°C (Ali et al., 1994). Wheat germination may occur between 4°C and 37°C and the optimal temperature is about 25°C (Ali et al., 1994). Wheat seed takes approximately 105 degree days(°Cd) to germinate and emerge from a seeding depth of less than 2.54 cm (Fowler, 2002). During germination, the seminal roots emerge and grow first, followed by the coleoptiles which protect the emergence of the first leaf. The emergence of coleoptiles is also affected by temperatures (Edward, 2008). In high temperatures coleoptiles length will be shortened and this will affect the emergence of seedlings. When sown, the seed embryo has 3-4 leaf primordial(Baker and Gallagher, 1983a). Two root systems are presents in wheat plants, the seminal roots and nodal roots. Seminal root systems grows from root primordia in the embryo, while nodal roots arise from the lower nodes of the plants (Kirby, 2002). Extensive distribution of roots through the soil and the large surface area of the root hairs make the wheat plant efficient and drought-resistant.

Emergence to double ridge

Double ridge is the first visible sign of the transition of the stem apex from the vegetative stage to the reproductive stage. By this time production of leaf primordia ceases and the apex commences to produce the reproductive structures of the spike. The time of double ridge influences the time of flowering of wheat.

The duration of the vegetative stage in wheat varies from 20 to 150 days depending on genotype and environmental factors. The main controls of this period are the length of the basic vegetative phase (BVP, also called inherent earliness) and the sensitivity to daylength and vernalisation. All of these are under genetic control and their combination and interaction with environmental conditions determines the time to double ridge. In tropical regions, response to vernalisation is not important as the temperatures are not low enough to satisfy even a low vernalisation requirement. Therefore, spring wheats, which have no response to vernalisation, are required in the tropics. Time to flower will depend on the sensitivity to photoperiod, the BVP and the response to temperature. Sensitivity to photoperiod differs among genotypes. Most cultivated wheats are quantitative long-day plants. Wheat will flower faster as the day-length increases, but does not require a particular length of day to induce flowering (Acevedo et al., 2002). High temperature during this phase can also reduce the time from emergence to double ridge(Shpiler and Blum, 1986).

The pattern of development will also influence tillering and biomass production in crops. All new growth on a wheat plant come from the shoot apical meristem, also called the growing point, and the timing of double ridge determines the final leaf number on the plant. Tillers develop from nodal buds in the axils of leaves. Tillers emerge systematically. The first tiller emerges from the axil of leaf 3 and subsequently primary tillers rise from leaf axils of the main shoot. Secondary tillers rise from the axils of leaves of primary tillers, and so on. Tiller appearance generally stops just before the beginning of stem elongation (Baker and Gallagher, 1983b). Longnecker et al. (1993), however, suggest that tillering is controlled by a number of genetic and environmental factors and does not stop at any specific wheat development stage. However the number of tillers is related to leaf appearance and to the maturity of the crop. It would be anticipated that the rapid development of wheat in warm tropical environments would limit tiller production by wheat.

Tillering has great agronomic importance in cereals since it may partially or totally compensate for any differences in plant number after crop establishment. The number of tillers is determined by genotype, seeding rate, soil moisture and fertility, and temperature. Tillering can be encouraged by low plant density; fertilizing with nitrogen; and, where possible, irrigating if soil moisture is low (Acevedo et al., 2002). Not all tillers however produce spikes, many tillers, especially later emerging tillers, abort before anthesis (Gallagher and Biscoe, 1978).

Double ridge to anthesis

The period from double ridge to anthesis determines the size of the ear and the potential number of grains in an ear. Therefore this period has a major influence on the yield potential of the crop. The duration of the period and the rate of biomass production during this period will largely determine the yield potential of the crop.

Jointing, the development of nodes and internodes that form the stem of the wheat plant, begins when growth of the tillers is complete. This phase marks the external signs of change from vegetative growth to reproductive growth, even though the change at the apex has occurred earlier. Growth at this stage is important for several reasons. Growth of the internodes pushes the growing point above the soil. The change from vegetative to reproductive growth and the subsequent development of the spike is also when the maximum number of kernels formed in the spike is determined, causing the yield at harvest to be susceptible to stress at this stage (Paulsen, 1997).

Wheat apex changes from the vegetative to the reproductive stage usually when plants have 4-8 leaves in the main shoot.The length of the apex at this time is approximately 0.5 mm. After spike initiation the apex will develop spikelet primordia which include the glume and lemma primordia. The floret primordia are found in the axils of each lemma. Each spikelet primordial in the central part of the spike has from 8 to 12 floret primordia, while spikelets at the basal and distal spike have from 6 to 8 florets. Less than half of these florets develop until anthesis; the other half will abort or are insufficiently developed to be fertilized at anthesis (Kirby and Appleyard, 1987; Hay and Kirby, 1991).

Early in reproductive development, terminal spikelet initiation occurs. At this stage, the growing apex is about 4 mm in length with 7 to 12 leaves in the main shoot. Spikelet number per spike is already determined at this stage, varying from 20 to 30 spikelet/spike (Kirby and Appleyard, 1987). Rahman et al.(1977)reported a positive correlation between the length of the vegetative phase and the number of spikelets per spike; lengthening the duration of the vegetative stage of the apex induces more spikelets per spike. However, the actual number of spikelets is determined by the length of the reproductive phase. This stage is particularly sensitive to environmental stresses, especially nitrogen and water (Wuest and Cassman, 1992). Masle (1984)and Kirby et al. (1985) point out that the terminal spikelet occurs in the field when the spike is at about 1 cm above the crown of the plant, however this is not easy to detect unless the plant apex is dissected.

After the terminal spikelet is formed, the stem starts to elongate and the spike begins to grow. The period of most rapid spike growth occurs from the appearance of the leaf prior to the flag leaf up to ten days after anthesis (Kirby and Appleyard, 1987). Spike growth develops slowly in its early stages, and increases greatly about the time when the ligule of the flag leaf become visible (Krumm et al., 1990). Crop growth rate during this period influences yield potential through its effect on the number of grain bearing sites. The effects of temperature and solar radiation on growth and yield can be integrated by calculating the photothermal quotient (PTQ) (Nix 1976) which is defined as:

$$\mathrm{PTQ} = \frac{R_n}{T_{mean}-4.5} \text{ (Fischer, 1985a).}$$

where R_n is the mean daily solar radiation and T_{mean} is the mean daily temperature during thecritical period of growth. Solar radiation influences crop growth rate and temperature affects rate of development, so the PTQ can be considered as an index of growth rate per unit of developmental time. For example Fischer (1985a) found a close relation between the number of kernels per unit area and PTQ during the 30 days before anthesis. High temperatures during floral initiation and spikelet development, a period of several weeks before anthesis, reduce the potential number of grains that determine maximum yield potential. This is associated with a shorter duration of the phase which may limit the number of spikelets and florets formed as well as by fertilization problem, as temperatures above 30°C during floret formation cause complete sterility (Saini and Aspinall, 1982). Higher radiation increases the amount of photosynthates available for spike growth, and lower temperatures prolong the period of spikelet growth and decrease competition for carbohydrates.

The duration of the phase is controlled genetically as well as being affected by environmental factors, mainly temperature. Maintaining the duration of this phase in tropical environments may assist in the production of high yields.

Anthesis to physiological maturity

The wheat spike contains only one spikelet per rachis node. Each spikelet has between 3 and 6 potentially fertile florets (Kirby and Appleyard, 1987), which are self-pollinated in most of the cases. Anthesis begins in the central part of the spike and continues towards the basal and apical parts during a 3-5 day period. The proximal florets of the central spikelet are fertilized two to four days earlier than the distal florets.

After floret fertilization, cellular division is rapid, during which the endosperm cells and amyloplasts are formed. This period is known as the lag phase and lasts for about 20 to 30 percent of the grain filling period. After this there is a phase of cell growth, and differentiation and starch deposition in the endosperm, which corresponds to linear grain growth and takes from 50 to 70 percent of the grain filling period. The embryo is formed at the time of endosperm growth (Jones et al., 1985).

A detailed study on the effect of high temperature to each developmental stage has been done by Amores-Vergara and Cartwright (1984). However, their individual effect to yield was not observed. It was stated that the duration of any stage was very closely related to current temperature, but was not affected by exposure to high temperatures at the previous developmental stages. It was also found that high temperature (27°C) during anthesis to physiological maturity shortens this stage drastically (16 days compared to 45 days at control 17°C).

Fischer (1985b) argues that increasing the length of the growing season will be a key factor for high yield in high temperature environments, such as those of the tropics. It is true that the longer growing season will affect the length of photosynthesis, which in turn will be beneficial for yield. However, since high temperature reduces the duration of growing period, it is important to determine which period is the most affected and which period give a great contribution to yield in environments such as Lombok where temperatures and day-length remain constant throughout the year. The importance of time of sowing could be a major control of the length of growing season.

4. EARLY AND LATE MATURING CULTIVARS

The importance of the optimal time of sowing of wheat for specific wheat-growing areas has been long-recognised in Australia and other wheat growing areas around the world (Coventry et al., 1993; Eagles et al., 2009). It isalso important thatthe phasic development of genotypes match with the environmental constraints of a region to avoid stress during the critical stage of development, such as rainfall distribution, changes in temperature and timing of stress events such as the incidence of frost, as well as the range of sowing times that are possible. This may mean developing appropriate combinations of crop maturity and sowing time within the growing season of the region. In the tropics, sowing times will be influenced, to a large degree, by the need to grow wheat when temperatures are low. The actual sowing time in a particular region variesdepending onthe characteristics of the season as well as specific soil and cultural requirements of a variety. The maturity type of a genotype will also influence its optimum sowing time.

Cultivars with different maturity types may vary in their adaptation to some stresses such as heat stress. For example, Tewolde et al.(2006)found that early heading cultivars could perform better compared to later heading cultivars when heat stress occurred after anthesis. This was due to three reasons. Firstly, the early-heading cultivars have a longer post-heading period and, therefore, longer grain filling time than the later-heading cultivars. Secondly, early-heading cultivars completed grain filling earlier in the season when air temperatures are lower and generally more favourable and thereby escape the most severe effects of heat stress. Finally, early heading cultivars retained more green leaves and lost fewer leaves to senescence at anthesis compared to later-heading cultivars, although earlier-heading cultivars produced fewer total leaves per tillers. Therefore, early heading is important and effective in wheat cultivars adapted to regions where high temperature stress progressively develops during the post-heading period (Tewolde et al., 2006). However, on Lombok Island, where there are high and constant temperatures throughout the year, increasing heat stress after anthesis will not occur and so the value of early maturity to escape heat stress will be limited. Despite a lack of a large seasonal variation in temperature (as well as photoperiod), the maturity type of a variety may still be important to adaptation and yield on Lombok to allow full use of the growing season. The timing and length of developmental phases such as tillering, stem elongation, ear emergence, anthesis and ripening will determine the biomass production and yield of wheat and each has a different level of tolerance to high temperatures. The timing of these growth stages is controlled by the developmental genes of a variety(Kosner and Pankova, 1998) and a variety's combination of developmental genes will influence how well it is adapted to the growing seasons on Lombok. For example, at one extreme a very late flowering variety may flower too late to allow the crop to fill grain and mature before the rainy season commences, while at the other extreme a very early flowering variety may develop so rapidly that yield is limited by low biomass production. As well, since crops on Lombok will be growing on residual soil moisture after rice, minimising terminal water stress may be a more important factor influencing the value of different maturity type's lines. Previous work in Indonesia did not examine the importance of maturity type and its interaction with sowing time, which is an important aspect of adaptation of wheat to tropical regions.

5. THE INFLUENCE OF PHOTOPERIOD, VERNALISATION AND BASIC VEGETATIVE PHASE ON WHEAT GROWTH AND DEVELOPMENT

The correct timing of phenological events is arguably the most important factor for adaptation and high yield in a particular environment. The environment strongly influences the physiological mechanisms that trigger the transition of phases in crop growth and development. However, the effect of these environmental factors such as photoperiod and temperature varies among cultivars. Therefore knowledge of crop growth and developments related to environmental influences are essential in many agronomic applications, including crop adaptation to different environments.

Temperature and photoperiod are among the environmental components that most affect plant growth and development (Slafer and Rawson, 1994; Snape et al., 2001). Yield is affected by sowing time and location because of the differences in temperature and photoperiod during the year and among different locations which influence rates of development. Changes in sowing date can alter the duration of some developmental stages significantly, and to different degrees depending on cultivars (Angus et al., 1981; Hay and Wilson, 1982a; Kirby et al., 1985; Savin and Nicolas, 1996), while Bauer et al. (1988) pointed to the location where crops were grown as an important influence on development.

Basic vegetative phase (BVP), inherent earliness or earliness *per se* is another characteristic controlling wheat development and growth which is independent of photoperiod and vernalisation (Slafer, 1996; Appendino and Slafer, 2003).

Depending on the requirement of vernalisation to promote flowering,wheat can be classified into winter and spring types. Major genes controlling sensitivity to vernalisation, the *Vrn* genes, determine the spring wheat or winter wheat difference: The lack of vernalisation requirement defines a spring type (Snape et al., 2001).

Vernalisation and photoperiod affect time of floral initiation, timeof developmental stages up to flag leaf stage, as well as leaf number and tiller number and spikelet number in sensitive genotypes (Levy and Peterson, 1972; Worland, 1996; Whitechurch and Snape, 2003). Earliness *per se* is the variation in flowering time of plants independent of vernalisation and photoperiod (Snape et al., 2001).

The response to vernalisation is mainly controlled by Vrn-A1, Vrn-B1, and Vrn-D1 genes located on the 5A, 5B and 5D chromosomes (Law et al., 1976; Eagles et al., 2009; Eagles et al., 2010). Genes Ppd-A1, Ppd-B1 and Ppd-D1, located on group 2 chromosomes primarily control sensitivity to photoperiod (Eagles et al., 2009; Eagles et al., 2010).

Midmore et al. (1982) compared wheat development and growth at a number of tropical locations. The growth of most genotypes was much faster at warm sites compared to the cool sites and consequently the duration of plant development was generally shorter under the hotter conditions, irrespective of daylength or vernalisation sensitivities (Midmore et al., 1982). The vernalisation-responsive cultivars delayed initiation of the terminal spikelet due to the lack of cold, and grew more leaves, spikelets and tillers compared to non-responsive cultivars at warm sites. Photoperiod sensitivity was important as the photoperiod-sensitive cultivars may delay development rate beyond terminal spikelet initiation (Midmore et al., 1982).

6 LIMITATION OF WHEAT PRODUCTION IN TROPICAL/SUBTROPICAL ENVIRONMENTS

Wheat is a temperate plant, therefore when grown in the warm tropics it faces various limitations. The major limitations to wheat growth in the tropics are related to temperature, moisture and soil properties (Fischer, 1985b; Wall, 1987). High temperatures affect plant growth rate and if sufficiently high, can cause heat stress. Drought is another limitation of agricultural practice in the tropics. The timing of the end and beginning of the rainy season, which determines the wheat growing season, is variable. Heavy rain early in the wheat-growing season could increase the risk of water logging (exacerbated by the poor soil structure left after a rice crop) while rain at the end of the season can cause grains to sprout before harvesting. Aluminium toxicity and phosphorus, boron and zinc deficiency are common in the soils of tropical areas (Wall, 1987). Biotic stresses can also be important with the warm and often humid conditions being conducive to insects and diseases.

In the tropical and subtropical areas where there is seasonal variation in temperature, and where winters are short, wheat is commonly sown when temperature are still high in order to achieve plant growth, especially flowering, during the coldest part of the year (Tahir et al., 2008), Growing wheat on Lombok should consider flowering time to happen during the coldest time of the year. In very low latitude regions, the seasonal variation in temperature is small, but consistently high. This high temperature is one of the main factors limiting the growth of wheat in tropical areas. To predict the impact of stress on plants, there are several things that need to be considered, including the temporal variations of the stress, the plant's ability to adapt to the stress, the timing of the stress in relation to the growth stage of the crop and the interaction between stresses (Jones et al., 1989).

7 EFFECTS OF HIGH TEMPERATURE STRESS

Wheat growth shows a characteristic response to temperature, with three regions being defined: suboptimal, optimum, and supra optimal. The optimum temperature varies with different growth stages and generally increases with later growth stages (Summerfield et al., 1991). Rates of development can be slowed at both sub– and supra-optimal temperatures. For example, the rate of progress towards flowering increases with increase in temperature to an optimum (18-24°C; reviewed by Porter and Gawit (1999)) at which flowering is most rapid; and at supra-optimal temperatures flowering is progressively delayed as temperatures become higher (Summerfield et al., 1991).

General responses of plant growth to high temperatures

A major problem of wheat growing in the tropics is heat stress which can reduce plant yield significantly. Certain plant development stages are known to be more sensitive to heat stress than others (Fischer and Byerlee, 1991) and so the timing of stress relative to these sensitive growth stages will determine the loss of yield. The acceleration of plant growth and development will only speed up in the range leading up to the optimumtemperature then can slow at veryhigh temperatures which subsequently reduces plant size, such as leaves, tiller, spike, and consequently reduces plant yield (Fischer, 1985b; Shpiler and Blum, 1986; Wahid et al., 2007). High temperature stress may induce modification of plant physiological processes such as photosynthetic production directly (by affecting gas exchange and CO_2 fixation) or indirectly through modification of growth pattern in different phenological stages which may affect the photosynthetic area.

Growth of wheat during all development phases can be influenced by temperature (Slafer and Rawson, 1994). However, temperature sensitivity varies not only between plant organs but also during phenological development. There is also a some variation in the data of cardinal temperature of development stages as reviewed by Porter and Gawith

(1999). For example, the base temperature for anthesis is reported as 9.5°C (Slafer and Savin, 1991) or <10°C (MacDowell, 1973; Russell and Wilson, 1994), while maximum temperature were >30°C (MacDowell, 1973) or >32°C (Russell and Wilson, 1994). Nevertheless the period leading up to flowering is still the most sensitive to heat because it coincides with an important yield forming period.

Plant physiological changes in response to heat stress is one of the indicators of plant interactions with the environment. In tropical environments temperatures are generally higher than the optimum at all stages of the crop's growth, but especially during the pre-anthesis period, compared to the more temperature regions where wheat is more commonly grown. Different phenological stages have different sensitivities to high temperature, although the response differs among genotypes. The development stages at which heat stress occurs may determine the severity of damage to the crops. During the vegetative stage for example, heat stress can damage leaf properties which consequently may affect photosynthesis and biomass production. During the reproductive stage, heat stress is related to flower abortion and decreased grain set (Wahid et al., 2007), while heat stress during grain filling will reduce grain weight. Wheat genotypes have different responses to high temperature during germination, vegetative growth and reproductive stages (Rawson, 1986) although the period of ear development leading up to flowering is generally considered to be the most sensitive period for heat stress (Fischer, 1975). Consequently, managing the crop to minimise the impact of heat stress at this time may be an important aspect of management.

Germination

Management of wheat growing in the tropics may include avoiding the occurrence of heat stress at the time of critical stage of plant development and at the time of maximum water use, and this could be achieved with early sowing. In tropical environments, wheat is often sown at a time when air and soil temperatures are high. However, this hot season sowing may affect wheat germination and seedlings establishment (Hay and Wilson, 1982b; Ishag and Mohamed, 1996; Tahir et al., 2008).

Temperature is known to affect germination of wheat and wheat genotypes differ in their responses to temperature. High temperature during germination causes poor seedling establishment because of loss of viability of seed during imbibition and carbohydrate starvation and mobilisation into the developing seedling. Rate of germination increases linearly with temperature from a base temperature (T_b) to an optimum (T_{opt}), and then it declines to zero at the maximum temperature (T_{max}).

Optimum temperature is needed for the best germination process to occur, while extremely high temperature weakens the process and tends to delay germination. Various studies shows that the optimum temperature for sowing to emergence was about 20-25°C and the maximum temperatures tolerated were 30-38°C (Addae and Pearson, 1992; Ali et al., 1994; Porter and Gawith, 1999). However, while an optimum temperature is frequently cited, reasonably high germination may occur over a wide range of temperatures, which illustratesthe variation in cardinal temperature of wheat germination depending on variation of other factors such as variety. Ali et al.(1994) for example, reported all genotypes had maximum cumulative germination greater than 80% at less than 30 hours after sowing in temperatures between 10°C and 32°C. Germination was reduced by temperatures above 32°C, and at 36°C it was only about 30% at 90 hours after sowing. Apart from germination, coleoptile length is also shortened under high temperature. These short coleoptiles can affect plant establishment and influence the depth of sowing. Even though Lombok's average maximum temperature on July-August is still below the maximum temperature that germinating wheat seed can tolerate, the high temperature could affect wheat germination and establishment.

Root growth

The warm dry conditions during crop establishment and early growth in the tropics may result in roots being exposed to high temperatures especially when there is incomplete ground covering. Tahir et al. (2008) found a varied response of heat stress within plant vegetative growth in which root growth was affected by heat while for shoot growth this was not the case. High temperature up to 35°C significantly reduced root dry weight and root length, but increased root specific weight (Wardlaw and Moncur, 1995; Tahir et al., 2008). This indicates that secondary roots and root hairs are sensitive to high temperatures. Using Creeping bentgrass (*Agrostis palustris* Huds), Huang and Xu (2000) also found similar results; high temperature of 35°C significantly reduced root fresh weight and root number and increases root mortality.

High soil temperature has been found to be more damaging than high air temperature in limiting plant growth and physiological processes in various species (Kuroyanagi and Paulsen, 1988; Huang and Xu, 2000). Root growth may be affected more severely than shoot growth at high temperatures since roots have a lower optimum temperature requirement. The optimum temperature was below 16°C compared to around 20°C for shoot growth (Porter and Gawith, 1999).

In potato, damage to the root system caused by high soil temperature is one of the important factor causing depression of shoot growth at high temperatures (Sattelmacher et al., 1990). Possible cause for the plant growth effect by high soil temperature is direct damage to the roots which is responsible for inhibition of water uptake (Huang et al., 1991), and reductions in nutrient uptake and translocation (Papadopoulos and Tiessen, 1987).

Vegetative growth

Plant growth and development are affected by temperature. Temperature that is lower or higher than adaptable temperature ranges will affect wheat growth and development adversely and could cause a reduction in dry matter and yield. When temperatures are extremely lower or higher than the optimum, wheat production processes could cease (Porter and Gawith, 1999).

Leaf appearance and leaf size are strongly influenced by temperature. Rates of leaf appearance increase up to the optimum temperature but declines thereafter. Sensitivity to heat stress during vegetative growth is expressed as a reduction of leaf area and total leaf number (Midmore et al., 1984) and leaf dry weight (Tahir et al., 2009). The most important effect of high temperature is decreasing photosynthetic activity, chlorophyll accumulation and consequently decrease shoot and root growth (Kuroyanagi and Paulsen, 1988). Together, all of these effects of high temperature will reduce total photosynthetic production and biomass accumulation by the crop, which can lead to a substantial reduction in grain yield.

Although, there is some variation in temperature sensitivity between plant organs, the variation is still in a fairly narrow range, so that there is no strong evidence of variability on the temperature sensitivity. For example, the optimum temperature for leaf emergence was 21.3°C to 24.3°C (Cao and Moss, 1989), and other researchers found the maximum temperature at the time before leaf emergence is 25°C (Slafer and Rawson, 1994). Slafer and Rawson (1994) also found that the maximum temperature for stem elongation was 21°C.

Most of the experiments on the effects of high temperature have related to the flowering and grain filling, and there is limited information on its effect on vegetative growth and early reproductive development. This is because in the traditional wheat-growing regions, high temperature stress is important late in the growing season, during flowering to physiological maturity. However, in tropical regions such as Lombok, high temperatures may persist for long periods of time earlier in the growing season. The response to and the effect of this continuous high temperature on wheat yield are not well documented.

Anthesis

Pollen development and fertilisation is a critical stage of development of cereals and heat stress at this stage can cause large reductions in yield. The production and transfer of viable pollen to the stigma, germination of the pollen, growth of the pollen tube to the stylus, and fertilisation and development of zygote are necessary for successful seed set. Although all of these phases are temperature sensitive, some are more sensitive than others, and high temperature can cause sterility of male and female floret (Saini and Aspinall, 1982)

Pollen viability is very sensitive to heat stress. Heat stress immediately before anthesis reduces grain yield due to sterile pollen (Tashiro and Wardlaw, 1990; Wheeler et al., 1996b). The critical temperature for pollen viability in wheat is 30°C (Saini and Aspinall, 1982), lower than that of rice (34°C) (Stone, 2001). Three days exposure to 30°C during pollen mother cell meiosis (the ear still within leaf sheath) can reduce grain set in wheat by almost 70% while in rice there was only a 20% reduced. This reduction of grain set is caused by high pollen sterility. Heat stress does not affect the function of stigma (Dawson and Wardlaw, 1989); however, the hormonal signal which guides germination of the pollen tube to the ovule is disturbed, causing failure of fertilisation even if viable pollen is available (Stone, 2001). High temperature during meiosis and pollination is a potential problem in many tropical regions. On Lombok Island, maximum temperatures are generally within the range 25°- 30°C in the lowland areas (Fig 2.2). These are temperatures at which pollen viability may become a limitation.

Grain growth

Heat stress after anthesis reduces the grain filling duration, grain weight and spike weight of wheat, but generally does not change grain number (Shpiler and Blum, 1986; Wardlaw, 2002; Mohammadi et al., 2004). The optimal temperature for wheat from anthesis to maturity is 25ºC or lower (Fayerherm and Paulsen, 1981; Porter and Gawith, 1999). However, temperatures in many tropical and subtropical regions may be greater than this and so there may be significant reductions in grain weight. Gibson and Paulsen (1999) found that heat stress from 15-20 days after anthesis to maturity decreases grain weight up to 18%. Acevedo et al. (1991) observed 4% reduction in grain weight for each centigrade increase in mean air temperature during grain-filling, over a range of 17 to 24°C.

Wheat grain growth comprises 3 phases. During the initial phase, immediately after anthesis for about 4-6 days, cell division occurs and there is little change in grain size or grain dry weight. Grain dry weight then increases rapidly during the grain filling until maximum dry weight is achieved and the grain reaches physiological maturity. During the final phase grain dry weight remains stable until grain dries (Hunt et al., 1991; Wheeler et al., 1996b). Grain dry weight increases as a linear function of time during the grain filling phase, which means that grain dry weight is a product of the duration and rate of grain filling, and therefore the effect of environment on these component will determined final grain weight (Wheeler et al., 1996b).

The reduction in grain weight is related to the effects of temperature on the rate and duration of grain filling. The optimum temperature of grain filling is low, approximately 15-18°C. At higher temperatures the duration of grain growth is reduced but the rate of grain filling is increased (Nicolas et al., 1984; Hunt et al., 1991; Jenner, 1991; Wheeler et al., 1996b). At moderately high temperatures (approximately 15-25°C), there may be considerable compensation between the rate and the duration of grain filling with the consequence that there may be relatively little change in final grain weight. As temperatures increase further, up to approximately 27°C (day time maximum 30°C), there is only a marginal increase in the rate of grain filling and a significant reduction in the duration of grain filling, resulting in smaller grain at maturity (Shpiler and Blum, 1986; Tashiro and Wardlaw, 1990; Wardlaw, 2002). The effect is similar to that observed with drought, but while drought stress may impose a source limitation on grain filling associated with the availability of both current and stored photosynthate, high temperature normally appears to act directly on the developing grain in a spike (Wardlaw et al., 1980; Bhullar and Jenner, 1983; Wardlaw, 2002). However, at very high temperatures (greater than 30°C), both the rate of grain filling and the duration of grain filling can be reduced causing large reductions in grain weight.

8 DROUGHT STRESS

Drought is likely to be an important limiting factor for crop production for wheat on Lombok. There are different types of drought which are related to the latitude, temperature, and seasonal precipitation (Fischer and Turner, 1978). On Lombok, if wheat is grown during the dry season as the third crop after two rice crops, it will rely on residual soil moisture after the rice crops and grow under increasingly severe water stress, unless it is planted within areas with available water for irrigation. Drought during anthesis and grain filling may be important to yield depending on the amount of rainfall and the availability of irrigation water. A high degree of drought tolerance will therefore be an important characteristic of wheat varieties adapted to this farming system.

Plant responses to drought are complex and different mechanisms are adopted by plants in dry condition (Levitt, 1980; Jones et al., 1981). These mechanisms can be (1) drought escape by rapid development which allows plants to finish their cycle before severe water stress, (2) drought avoidance by two different mechanism, increasing water uptake (with vigorous and extensive root growth),or reducing transpiration rate (with reduction of stomatal conductance and leaf area), and (3) drought tolerance by maintaining tissue turgor during water stress via osmotic adjustment which allows plants to maintain growth.

The maintenance of high plant water status and plant functions at low plant water potential, and the recovery of plant function after water stress are the major physiological processes that contribute to the maintenance of high yield under cyclic drought periods (Blum, 1996). In a recent comparison of varieties showing different levels of tolerance to drought, Izanloo (2008) concluded that high stomatal conductance, low ABA content, and the capacity for osmotic adjustment were the main physiological attributes associated with tolerance under water stress which enabled plants to recover from water stress.

Wiegand et al.(1981) reported decreases in the rate of leaf appearance as the season progressed for some winter wheat cultivars grown in the subtropics. Drought stress can reduce the rate of leaf initiation (Husain and Aspinall, 1970; Clough and Milthorpe, 1975) and leaf expansion (Acevedo et al., 1971; Watts, 1974). Angus and Moncur (1977) reported an acceleration of phenological development in wheat with mild drought stress and delayed development with severe drought stress.

Root development can also be affected by drought. Drought can have a variety of effects on root growthdepending on the timing and severity of stress. Drought stress caused roots to develop slowly while the amount of roots decreased. Consequently, rooting ability was greatly affected in the jointing-flowering stage. The dry matter accumulation in roots also declined and the peak appearance was delayed (Zhou et al., 2000). Hurd (1968) demonstrated that root could penetrated more quickly in dry soil than in wet soil. Root growth was used in wheat breeding for drought resistance (Hurd, 1974; Passioura, 1983; Siddique et al., 1990).

Drought occurring after heading has little effect on the rate of grain filling, but grain growth duration (time from fertilization to maturity) is shortened and grain dry weight at maturity is reduced (Aggarwal and Sinha, 1984; Wardlaw, 2002). The reduction in net CO_2 exchange of the leaves, stems and ears of wheat following anthesis is accelerated under drought, with the possibility of a deficit of carbohydrate during grain filling. Part of the response to drought is an earlier mobilization of non-structural reserve carbohydrates from the stem and leaf sheaths, which provide a greater proportion of the kernel dry weight at maturity (Blum et al., 1991; Wardlaw, 2002).

The effect of high temperature is more severe when combined with drought stress. Drought and drought x heat reduces the storage capacity of the grain (Nicolas et al., 1984). The degree of reduction in storage capacity and subsequent accumulation of dry matter depended on the intensity and timing of water deficit. Water deficit was more severe when high temperature was combined with drought, and maximum cell number is reduced by 50-60% under drought x heat conditions. The reduction in final grain weight was partly due to a shorter duration of grain growth in the drought x heat treatments (Nicolas et al., 1984).

9. PHYSIOLOGICAL PROCESESS AND HEAT STRESS

High temperature has been known as a major environmental factor limiting wheat production in the tropical environments (Wheeler et al., 1996a; Ferris et al., 1998; Gibson and Paulsen, 1999). However, the yield reduction could be mediated by disruption of several physiological process.

Heat stress affects various basic physiological process such as photosynthesis, respiration and water relations (Wahid et al., 2007). Photosynthesis is sensitive to temperature, high temperature affects net photosynthetic (Pn), stomatal conductance (gs) and respiratory processes (Taiz and Zeiger, 2002) and these factors are correlated to yield (Fischer *et al.*, 1998). Reduction of photosynthesis at high temperature may be an important factor limiting productivity of wheat in tropical environments. This is because under such conditions plants tend to use resources to cope with the heat stress and therefore limited photosynthates would be available for growth such as for grain number and grain filling.The ability of plant species to acclimate to high temperatures has been found to be closely associated with the acclimation capacity at the photosynthesis level (Pearcy, 1978).

Understanding the response of photosynthesis to the increase of temperature is important for predicting the yield of wheat in tropical areas especially at low elevation. The rate of photosynthesis is determined primarily by temperature, the amount of light, and the availability of water and nutrients. When other factors are not limited, then temperature is responsible in affeting wheat production in the tropics.

High temperature significantly reduces photosynthetic rate, chlorophyll content and Rubisco activity at all development stages, however, the rate of reduction is more in heat susceptible genotypes. Heat tolerant genotypes shows less reduction in photosynthesis and maintained respiration (Almeselmani et al., 2012). Reduction in photosynthetic rate is known to be correlated with reduction in Rubisco activity as a response to the temperature stress (Salvucci and Crafts-Brandner, 2004).

Photosynthesis and remobilisation of stored water soluble carbohydrate (WSC) are the two major sources of carbon during grain filling period (McIntyre et al., 2011). WSC can make a significant contribution to final grain yield of about 10–20% at relatively non-stressed conditions (Gebbing et al., 1999), but under reduced photosynthesis, WSC increase its contribution to final yield to 50% or more (van Herwaarden et al., 1998; Rebetzke et al., 2008; Rattey et al., 2009). Remobilisation of WSC stored temporarily in the wheat stem ensures the supply of carbon to the grain when the rate of photosynthesis declines (Blum et al., 1994; van Herwaarden et al., 1998). Therefore, WSC is regarded as an important factor determining yield especially under conditions where photosynthesis is limited, such as at high temperature. WSC also shows important roles in osmotic regulation of cells under heat stress (Bolarin *et al.*, 1995). Ruuska *et al.*, (2006) found that genetic variation exists for WSC accumulation in the stems at anthesis.

10. OTHER CONSTRAINTS TO YIELD: NUTRITIONAL CONSTRAINTS, WATERLOGGING AND DISEASE

Nutritional constraints

The productivity of soil is determined by its fertility which is related to the contents of organic matter and nutrients stored. Loss of soil productivity is therefore related with the loss of organic matter and nutrient contents. Nutritional disorder is another problem of wheat growing and production in the tropics; some of tropical soils have low organic matter and are deficient in phosphorus, boron and zinc, and have a high concentration of aluminium that causes toxicity.

Wheat, similarly with other cereals, is considered as plant that has a low boron requirement. Wheat was continuing to grow under experimental condition without showing symptoms of deficiency while other crop species were affected (Rerkasem and Jamjod, 2004). However, boron deficiency has been observed in the field with symptoms of male sterility in various different places such as Brazil, Nepal and China (Rerkasem and Jamjod, 2004).

The first response to boron detected in deficient higher plants is the cessation of root elongation (Dell and Huang, 1977; Rerkasem and Jamjod, 2004). Boron deficiency is known to inhibit root elongation through limiting cell enlargement and cell division in the growing zone of root tips. This inability of cells to enlarge causes malformations of cell wall structure and the loss of plastic extensibility (Hu and Brown, 1994; Dell and Huang, 1997).

The cessation of root growth because of boron deficiency, however, is rarely seen in wheat (Rerkasem and Jamjod, 2004). Wheat seems to be more tolerant compared to most dicots. Snowball and Robson (1983) observed in a solution culture contain no boron that wheat roots can grow continuously for a considerable time while roots of subterranean clover (*Trifolium subterraneum*) stopped immediately.

Boron plays an important role in cell wall structure and plasticity as stated before (Hu and Brown, 1994; Dell and Huang, 1997), therefore, under boron deficiency plants will show impaired development of newly-initiated leaves. Plant leaves under limited boron will be small and if boron deficiency is prolonged, leaves become necrotic (Dell and Huang, 1997). Symptoms of boron deficiency in wheat show the young leaf with a longitudinal splitting close to the midrib and the development of a saw tooth effect on the margin, reflecting abnormal development of cells (Snowball and Robson, 1983).

Plant reproductive growth is affected more severely by boron deficiency. Plants grown in a boron deficient medium may not develop apical meristems normally, and consequently will not develop flowers. Boron deficient plants also develop sterile male flowers such as on wheat, rice and barley and in the other case female parts are sterile such as on maize and avocado (Dell and Huang, 1997). In wheat, male and female parts of flowers were affected on boron deficient plants (Rerkasem *et al,* 1993). Boron deficiency in wheat fields can be seen during anthesis when the floret remain open longer for a few days instead of only a few hours of normal plants (Dell and Huang, 1997; Rerkasem and Jamjod, 2004).

Boron deficiency is not considered an issue in Lombok's agricultural practice. Sofyan *et al.* (2004) reported the status of nitrogen, phosphorus, potassium and zinc of

Lombok's soil, and no information about boron content; however, there is no guarantee that boron deficiency is not a limitation of Lombok's agricultural productions process.

Zinc is an essential micronutrients required for the normal growth and development of plants. Zinc deficiency is the most widespread disorder and constitutes a major soil fertility problem in many areas (Singh, 1992). Zinc deficiency and heat stress during grain filling occur in a number of important wheat growing regions around the world. In a zinc deficient soil, our previous work demonstrated the importance of Zn uptake to the growth of the durum wheat genotypes which was shown by significant correlations between maximum uptake rates of zinc and maximum crop growth rate (Zubaidi *et al*, 1999).

The changes in grain protein composition due to high temperature are well documented, but little is known about the effect of grain Zn and its interaction with heat stress. Zubaidi *et al.* (1999) demonstrate that Zn nutrition can change protein composition and the effects of Zn may interact with grain filling temperatures.

Zn-efficient cultivars accumulated greater amounts of Zn in their shoots than inefficient cultivars, but no strong correlation between shoot Zn and shoot dry matter production was found. All the cultivars accumulated higher concentrations of iron, copper, manganese, and phosphorus at deficient levels of Zn, compared with adequate Zn concentrations. The Zn-inefficient cultivars accumulated higher concentrations of these other elements compared to Zn-efficient cultivars.

Deficiency in zinc is one of the limitations of wheat growing in the tropic (Wall, 1984). Further, high availability of phosphorus, which is commonly found on Lombok, could make the deficiency in zinc more severe in Lombok soils (Sofyan *et al.,* 2004) as Robson and Pitman (1983) found that increasing the availability of P in the soil can induce Zn deficiency.

Waterlogging

Waterlogging stress is another potential limiting factor influencing wheat production on Lombok. Heavy rainfall and inadequate soil drainage causes waterlogging to happen in wheat production sites espesially on Lombok that have a heay rainfall during the wet season. The problem can be made worse by the need to grow wheat after padi rice, which means that the soil structure is often poor. Waterlogging causes oxygen limitation which can reduce shoot and root growth, drymatter accumulation, and final grain yield.

In wheat the most sensitive period to waterlogging is during germination (Cannel et al, 1980). Waterlogging during this period reduced plant population by 12-38% during 6 days of waterlogging, and killed all seedling at 12 days of waterlogging (Cannel et al, 1980). Waterlogging at early growth stages caused great reductions in root, dry matter, and grain yield productions (Watson et al, 1976). Reductions by 41% of tiller number and 20% of kernel numbers were also found which then associated with 44% grain yield reductions (Collaue and Harrison, 2002). Yield reductions about 0.29t/ha was found to be associated with waterlogging during the 30 days before anthesis (McDonald and Gardner, 1987).

Diseases

Knowing pests and diseases that may cause injuries and are likely to affect plant health and quality is critical to minimizing the gap between attainable yield and actual yield. Disease epidemics result from the combination of inoculums, favourable environment and host susceptibility. Efforts to adapt wheat into non-traditional areas, but especially warm and more wet areas such as Indonesia, may have serious implications for disease management. The incidence of diseases caused by *Fusarium* spp., *Ustilago tritici*, *Drechslera sorokiana*, *Cladosporium* sp., *Sclerotium rolfsi*, *Puccinia recondita* have been detected in Java Island-Indonesia (Handoko, 2007). The incidence and severity of these diseases may be influenced by sowing date but little is known of this effect on Lombok.

11. RESEARCH ON WHEAT ADAPTATION ON LOMBOK ISLAND

As wheat production has now expanded into tropical areas,studies on wheat adaptation to the tropical areasstill need to be done. While tropical environments are characterised by warm to hot growing seasons and fast rates of development, there can be variation in the intensity and magnitude of these effects due to latitude, altitude and local environmental conditions. There has been little recent work on adaptation of wheat to tropical regions and there has been no experimental study on adaptation of wheat in Lombok, which isone of the areas in Indonesia proposed for wheat growing. Although in these tropical environments wheat could be grown at high altitude to minimise the adverse effects of high temperature, this is not always possible since the areas are limited and the temperature is still relatively high compared to traditional wheat growing areas.

While there are a number of biotic and abiotic stresses that can affect wheat production in tropical environments, high temperature stress is pervasive and, arguable, is less able to be managed compared to disease, drought and nutrient stress. The general effects of high temperature on growth and development of wheat have been widely reviewed (Ferris et al., 1998; Gibson and Paulsen, 1999; Porter and Gawith, 1999; Stone and Nicolas, 1995; Wardlaw et al., 1980; Wheeler et al., 1996a; Wheller et al., 2000) although the majority of this work has not been focussed specifically on tropical environments. It is documented that heat stress is one of common abiotic factors responsible for reducing world yields in about 40% of the world's wheat producing areas, which cover 36 million hectares (Fischer and Byerlee, 1991). However, there are a number of aspects of this general effect that require further research work.

In the traditional wheat-growing areas of the world, high temperature stress mostly occurs late in the growing season, during flowering to physiological maturity. However, in tropical regions such as Lombok, high temperatures may persist for long periods of time from earlier in the growing season through to grain development. Research on wheat responses to heat stress hasoften examined effects of elevated temperature during specific developmental stages. However, there is relatively little information about plant growth and development, and especially early development, in a continuous high temperature typical of that found in tropical environments and the response to and effects of this continuous high temperature on wheat yield are not well documented. Much of the earlier work also examined a small group of genotypes, and the effects of some of the major developmental genes on responses to high temperatures are defined poorly.

Yield reduction of wheat in high temperature could be caused by several factors such as accelerated phenological development (Midmore et al., 1984) which would affect sink development by affecting development of the spike, reduction in photosynthesis and an increase in respiration (Reynolds et al., 1998; Reynolds et al., 2000; Almeselmani et al., 2012) which may limit biomass production and the allocation of C to the developing sink. Accelerated growth at continuous high temperature which willaffect phenological development such as times to double ridge, terminal spikelet initiation, and duration of spikelet primordial initiation as well as time to flowering of wheat,and their effects to yield need to be examined. There is a range of maturity types in wheat that are determined by the presence of major developmental genes and which will influence the durations of the major phenological phases of growth. Previous work in Indonesia did not examine the importance of maturity type and its interaction with sowing time, which is an important aspect of adaptation of wheat to tropical regions.

Most of the previous studies on the effects of temperature stress on growth and photosynthesis have examined short term effects or responses at specific growth stages, often focussed on the critical yield-determining periods around flowering and grain filling. There is no work that has examined responses in plants grown under prolonged exposure to high temperature.

Based on the review of past work the following questions arise

- How does early reproductive development respond to continuous high and supra-optimal temperature?
- How influential are the major developmental genes in moderating development under high temperatures?
- Can variation in sowing time among varieties with different patterns of development be exploited to improve wheat productivity on Lombok Island?
- What are the effects of continuous high temperature on plant biomass production and grain yield?

REFFERENCES

Acevedo, E., Hsiao, T.C., Henderson, D.W., 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiology 48, 631-636.

Acevedo, E., Nachit, M., Ortis-Ferrara, G., 1991. Effect of heat stress on wheat and possible selection tools for use in breebing for tolerance. Wheat for the nontraditional warm areas; Proceeding of an International Conference, Foz do Iguacu, Brazil, pp. 401-421.

Acevedo, E., Silva, P., Silva, H., 2002. Wheat growth and physiology. In: Curtis, B.C., Rajaram, S., MacPherson, H.G. (Eds.), Bread wheat; Improvement and Production. Food and Agriculture Organisation of The United Nations, Rome, Italy.

Addae, P.C., Pearson, C.J., 1992. Thermal requirement for germination and seedling growth of wheat. Australian Journal of Agricultural Research 43, 585-594.

Aggarwal, P.K., Sinha, S.K., 1984. Effect of water stress on grain growth and assimilate partitioning in two cultivars of wheat contrasting in their yield stability in a drought-environment. Annals of Botany 53, 329-340.

Ali, Z.I., Mahalakshmi, V., Singh, M., Ortiz-Ferrara, G., Peacock, J.M., 1994. Variation in cardinal temperatures for germination among wheat (*Triticum aestivum*) genotypes. Annals of Applied Biology 125, 367-375.

Alkhatib, K., Paulsen, G.M., 1990. Photosynthesis and Productivity during High-Temperature Stress of Wheat Genotypes from Major World Regions. Crop Science 30, 1127-1132.

Almeselmani, M., Deshmukh, P.S., Chinnusamy, V., 2012. Effect of prolonged high temperature stress on respiration, photosynthesis and gene expression in wheat

(*Triticum aestivum* L.) varieties differing in their thermotolerance. Plant Stress 6, 25-32.

Amores-Vergara, E., Cartwright, P.M., 1984. Effects of short periods of exposure to high temperature on the phenology and shoot apex development of wheat cv. Sonora 64. Australian Journal of Agricultural Research 35, 139-148.

Angus, J.F., Mackenzie, D.H., Morton, R., Schafer, C.A., 1981. Phasic development in field crops. II. Thermal and photoperiodic responses of spring wheat. Field Crops Research 4, 269-283.

Angus, J.F., Moncur, M.W., 1977. Water stress and phenology in wheat. Australian Journal of Agricultural Research 28, 177-181.

Appendino, M.L., Slafer, G.A., 2003. Earliness per se and its dependence upon temperature in diploid wheat lines differing in the major gene Eps-A m1 alleles. Journal of Agricultural Science 141, 149-154.

Baker, C.K., Gallagher, J.N., 1983a. The development of winter wheat in the field. 1. Relation between apical development and plant morphology within and between seasons. Journal of Agricultural Science, UK 101, 327-335.

Baker, C.K., Gallagher, J.N., 1983b. The development of winter wheat in the field. 2. The control of primordium initiation rate by temperature and photoperiod. Journal of Agricultural Science, UK 101, 337-344.

Bauer, A., Garcia, R., Kanemasu, E.T., Blad, B.L., Hatfield, J.L., Major, D.J., Reginato, R.J., Hubbard, K.G., 1988. Effect of latitude on phenology of "Colt" winter wheat. Agricultural and Forest Meteorology 44, 131-140.

Berry, J., Bjorkman, O., 1980. Photosynthetic Response and Adaptation to Temperature in Higher Plants. Annual Review of Plant Physiology and Plant Molecular Biology 31, 491-543.

Bhullar, S.S., Jenner, C.F., 1983. Responses to brief periods of elevated temperature in ears and grains of wheat. Australian Journal of Plant Physiology 10, 549-560.

Blum, A., 1986. The Effect of Heat Stress on Wheat Leaf and Ear Photosynthesis. Journal of Experimental Botany 37, 111-118.

Blum, A., 1996. Crop responses to drought and the interpretation of adaptation. Plant Growth Regulation 20, 135-148.

Blum, A., Shpiler, L., Golan, G., Mayer, J., Sinmena, B., 1991. Mass selection of wheat for grain filling without transient photosynthesis. Euphytica 54, 111-116.

Blum, A., Sinmena, B., Mayer, J., Golan, G., Shpiler, L., 1994. Stem Reserve Mobilisation Supports Wheat-Grain Filling Under Heat Stress. Australian Journal of Plant Physiology 21, 771-781.

Cannell R.Q. Belford R K., Gales K.,Dennis C.W. and Prew R D, 1980. Effects of Waterlogging at Different Stages of Development on the Growth and Yield of Winter Wheat. *J. Sci. Food Agric.* 1980, 31, 117-132

Cao, W.X., Moss, D.N., 1989. Temperature effect on leaf emergence and phyllochron in wheat and barley. Crop Science 29, 1018-1021.

Chettri, G.B., Ghimiray, M., Floyd, C.N., 2003. Effects of farmyard manure, fertilizers and green manuring in rice-wheat systems in Bhutan: results from a long-term experiment. Experimental Agriculture 39, 129-144.

Clough, B.F., Milthorpe, F.L., 1975. Effects of water deficit on leaf development in tobacco. Australian Journal of Plant Physiology 2, 291-300.

Collaku A. and Harrison S.A, 2002. Losses in Wheat Due to Waterlogging. Crop Sci. 42:444–450

Coventry, D.R., Reeves, T.G., Brooke, H.D., Cann, D.K., 1993. Influence of genotype, sowing date, and seeding rate on wheat development and yield. Australian Journal of Experimental Agriculture 33, 751-757.

Dawson, I.A., Wardlaw, I.F., 1989. The tolerance of wheat to high temperatures during reproductive growth. III. Booting to anthesis. Australian Journal of Agricultural Research 40, 965-980.

Eagles, H.A., Cane, K., Kuchel, H., Hollamby, G.J., Vallance, N., Eastwood, R.F., Gororo, N.N., Martin, P.J., 2010. Photoperiod and vernalization gene effects in southern Australian wheat. Crop & Pasture Science 61, 721-730.

Eagles, H.A., Cane, K., Vallance, N., 2009. The flow of alleles of important photoperiod and vernalisation genes through Australian wheat. Crop & Pasture Science 60, 646-657.

Edward, J., 2008. Factors Affecting Wheat Germination and Stand Establishment in Hot Soils Oklahoma Cooperative Extension Fact Sheets. Oklahoma State University, Oklahoma, pp. PSS-2256.

Fayerherm, A.M., Paulsen, G.M., 1981. Development of a wheat yield prediction model. Agronomy Journal 73, 277-282.

Ferris, R., Ellis, R.H., Wheeler, T.R., Hadley, P., 1998. Effect of High Temperature Stress at Anthesis on Grain Yield and Biomass of Field-grown Crops of Wheat. Annals of Botany 82, 631-639.

Fischer, R.A., 1975. Yield potential in dwarf spring wheat and the effect of shading. Crop Science 15, 607-613.

Fischer, R.A., 1985a. Number of kernels in wheat crops and the influence of solar radiation and temperature. Journal of Agricultural Science, UK 105, 447-461.

Fischer, R.A., 1985b. Physiological limitations to producing wheat in semitropical and tropical environments and possible selection criteria. Wheats for more tropical environments. A proceedings of an international symposium on wheat production and research in tropical environments, held in Mexico on 24-28 September, 1984. CIMMYT, Mexico, pp. 209-230.

Fischer, R.A., Byerlee, D.R., 1991. Trends of wheat production in the warmer areas: major issues and economic considerations.

Fischer, R.A., Turner, N.C., 1978. Plant productivity in the arid and semiarid zones. Annual Review of Plant Physiology 29, 277-317.

Fowler, D.B., 2002. Growth Stages of Wheat. Winter Cereals Productions. Crop Development Centre, University of Saskatchewan., Saskatoon, Canada.

Gallagher, J.N., Biscoe, P.V., 1978. A physiological analysis of cereal yield. II. Partitioning of drymatter. Agricultural Programs 53, 51-70.

Gebbing, T., Schnyder, H., Kuhbauch, W., 1999. The utilization of pre-anthesis reserves in grain filling of wheat. Assessment by steady-state (CO2)-C-13/(CO2)-C-12 labelling. Plant Cell and Environment 22, 851-858.

Gibson, L.R., Paulsen, G.M., 1999. Yield components of wheat grown under high temperature stress during reproductive growth. Crop Science 39, 1841-1846.

Gupta, P.K., Shivraj, S., Nahar, S., Dixit, C.K., Singh, D.P., Sharma, C., Tiwari, M.K., Gupta, R.K., Garg, S.C., 2004. Residue burning in rice-wheat cropping system: causes and implications. Current Science 87, 1713-1717.

Gusmayanti, E., Pertiwi, S., Handoko, Risdiyanto, I., Machida, T., 2006. Determining potential wheat growing areas in Indonesia by using the spatial compromise programming technique. Agricultural Information Research 15, 373-379.

Handoko, I., 2007. Gandum 2000: Penelitian pengenbangan gandum di Indonesia (Wheat 2000: Wheat research and development in Indonesia). SEAMEO_BIOTROP, Jakarta.

Hay, R.K.M., Kirby, E.J.M., 1991. Convergence and synchrony-a review of the coordination of development in wheat. Australian Journal of Agricultural Research 42, 661-700.

Hay, R.K.M., Wilson, G.T., 1982a. Leaf appearance and extension in field-grown winter wheat plants - The importance of soil-temperatur during vegetattive growth. Journal of Agricultural Science 99, 403-410.

Hay, R.K.M., Wilson, G.T., 1982b. Leaf appearance and extension in field-grown winter wheat plants: the importance of soil temperature during vegetative growth. Journal of Agricultural Science, UK 99, 403-410.

Huang, B., Xu, Q., 2000. Root growth and nutrient element status of creeping bentgrass cultivars differing in heat tolerance as influenced by supraoptimal shoot and root temperatures. Journal of Plant Nutrition 23, 979-990.

Huang, B.R., Taylor, H.M., McMichael, B.L., 1991. Effects of temperature on the development of metaxylem in primary wheat roots and its hydraulic consequence. Annals of Botany 67, 163-166.

Hunt, L.A., Poorten, G.v.d., Pararajasingham, S., 1991. Postanthesis temperature effects on duration and rate of grain filling in some winter and spring wheats. Canadian Journal of Plant Science 71, 609-617.

Hurd , E. A., 1968. Growth of Roots of Seven Varieties of Spring Wheat at High and Low Moisture Levels. Agronomy Journal 60, 201-205

Husain, I., Aspinall, D., 1970. Water stress and apical morphogenesis in barley. Annals of Botany 34, 393-407.

Ishag, H.M., Mohamed, B.A., 1996. Phasic development of spring wheat and stability of yield and its components in hot environments. Field Crops Research 46, 169-176.

Izanloo, A., Condon, A.G., Langridge, P., Tester, M., Schnurbusch, T., 2008. Different mechanisms of adaptation to cyclic water stress in two South Australian bread wheat cultivars. Journal of Experimental Botany 59, 3327-3346.

Jenner, C.F., 1991. Effects of exposure of wheat ears to high temperature on dry matter accumulation and carbohydrate metabolism in the grain of two cultivars. I. Immediate responses. Australian Journal of Plant Physiology 18, 165-177.

Jones, H.G., Flowers, T.J., Jones, M.B., 1989. Plant under stress. Cambridge University Press, Cambridge UK.

Jones, M.M., Turner, N.C., Osmond, C.B., 1981. Mechanisms of drought resistance. In: Paleg, L.G., Aspinall, D. (Eds.), The physiology and biochemistry of drought resistance in plants. Academic Press, pp. 15–35.

Jones, R.J., Roessler, J., Ouattar, S., 1985. Thermal environment during endosperm cell division in maize: effects on number of endosperm cells and starch granules. Crop Science 25, 830-834.

Khybri, M.L., Gupta, R.K., Sewa, R., Tomar, H.P.S., 1992. Crop yields of rice and wheat grown in rotation as intercrops with three tree species in the outer hills of Western Himalaya. Agroforestry Systems 17, 193-204.

Kirby, E.J.M., 2002. Botany of the wheat plants. In: Curtis, B.C., Rajaram, S., Macpherson, H.G. (Eds.), BREAD WHEAT, Improvement and Production. Food And Agriculture Organization Of The United Nations, Rome.

Kirby, E.J.M., Appleyard, M., 1987. Development and structure of the wheat plant. In: Lupton, F.G.H. (Ed.), Wheat breeding. Chapman and Hall, London, pp. 287-311.

Kirby, E.J.M., Appleyard, M., Fellowes, G., 1985. Variation in development of wheat and barley in response to sowing date and variety. Journal of Agricultural Science, UK 104, 383-396.

Klatt, A.R., 1988. Wheat Production Constraints in Tropical Environments; A Proceedings of the International Conference January 19-23, 1987 Chiang Mai, Thailand. CIMMYT, Mexico.

Kosner, J., Pankova, K., 1998. The detection of allelic variants at the recessive vrn loci of winter wheat. . Euphytica 101, 9-16.

Krumm, M., Moazami, V., Martin, P., 1990. IInfluence of potassium nutrition on concentrations of water soluble carbohyd-rates, potassium, calcium, and magnesium and the osmotic potential in sap extracted from wheat (Triticum aestivum) ears during pre-anthesis development. Plant and Soil 124, 281-285.

Kuroyanagi, T., Paulsen, G.M., 1988. Mediation of high-temperature injury by roots and shoots during reproductive growth of wheat. Plant, Cell & Environment 11, 517-523.

Law, C.N., Worland, A.J., Giorgi, B., 1976. The genetic control of ear-emergence time by chromosomes 5A and 5D of wheat. Heredity 36, 49-58.

Levitt, J., 1980. Stress terminology. In: Turner, N.C., Kramer, P.J. (Eds.), Adaptation of plants to water and high temperature stress. Wiley, New York, pp. 473–439.

Levy, J., Peterson, M.L., 1972. Responses of spring wheats to vernalization and photoperiod. Crop Science 12, 487-490.

Longnecker, N., Kirby, E.J.M., Robson, A., 1993. Leaf emergence, tiller growth, and apical development of nitrogen-deficient spring wheat. Crop Science 33, 154-160.

McDonald G. K. and Gardner W. K*., 1987.* Effect of waterlogging on the grain yield response of wheat to sowing date in south-western Victoria. *Aust. J. Exp.* Agric., 1987, 27, 661-70

MacDowell, F.D.H., 1973. Growth kinetics of Marquis Wheat. 5. Morphogenic dependence. Can. J. Bot. 51, 1259-1265.

Masle, J., 1984. Competition among tillers in winter wheat: consequences for growth and development of crop. In: day, W., Atkin, R.K. (Eds.), Wheat growth and modelling. Plenum Press, London.

McIntyre, C.L., Casu, R.E., Rattey, A., Dreccer, M.F., Kam, J.W., van Herwaarden, A.F., Shorter, R., Xue, G.P., 2011. Linked gene networks involved in nitrogen and carbon metabolism and levels of water-soluble carbohydrate accumulation in wheat stems. Functional & Integrative Genomics 11, 585-597.

Midmore, D.J., Cartwright, P.M., Fischer, R.A., 1982. Wheat in tropical environments. I. Phasic development and spike size. Field Crops Research 5, 185-200.

Midmore, D.J., Cartwright, P.M., Fischer, R.A., 1984. Wheat in tropical environments. II. Crop growth and grain yield. Field Crops Research 8, 207-227.

Mohammadi, V., Qannadha, M.R., Zali, A.A., Yazdi-Samadi, B., 2004. Effects of post-anthesis heat stress on the head traits of wheat. International Journal of Agriculture and Biology 6, 42-44.

Nicolas, M.E., Gleadow, R.M., Dalling, M.J., 1984. Effects of drought and high temperature on grain growth in wheat. Australian Journal of Plant Physiology 11, 553-566.

Papadopoulos, A.P., Tiessen, H., 1987. Root and air temperature effects on the elemental composition of tomato. Journal of the American Society for Horticultural Science 112, 988-993.

Paulsen, G.M., 1997. Growth and Development. Wheat Production Handbook. K-State Research & Extension, Manhattan, Kansas, pp. 2-5.

Pearcy, R.W., 1978. Effect of growth temperature on the fatty acid composition of the leaf lipid in *Artiflex lentiformis* (Torr.) wats. Plant Physiology 59, 873-878.

Porter, J.R., Gawith, M., 1999. Temperatures and the growth and development of wheat: a review. European Journal of Agronomy 10, 23-36.

Prasad, R., Gangaiah, B., Aipe, K.C., 1999. Effect of crop residue management in a rice-wheat cropping system on growth and yield of crops and on soil fertility. Experimental Agriculture 35, 427-435.

Rahman, M.S., Wilson, J.H., Aitken, Y., 1977. Determination of spikelet number in wheat. II. Effect of varying light level on ear development. Australian Journal of Agricultural Research 28, 575-581.

Rattey, A., Shorter, R., Chapman, S., Dreccer, F., van Herwaarden, A., 2009. Variation for and relationships among biomass and grain yield component traits conferring improved yield and grain weight in an elite wheat population grown in variable yield environments. Crop & Pasture Science 60, 717-729.

Rawson, H.M., 1986. High-temperature-tolerant wheat: a description of variation and a search for some limitations to productivity. Field Crops Research 14, 197-212.

Rawson, H.M., 1988. Effects of high temperatures on the development and yield of wheat and practices to reduce deleterious effects. In: Klatt, A.R. (Ed.), Wheat production constraints in tropical environments. Proceedings of the international conference, Chiang Mai, Thailand, 19-23 January 1987., pp. 44-62.

Rebetzke, G.J., van Herwaarden, A.F., Jenkins, C., Weiss, M., Lewis, D., Ruuska, S., Tabe, L., Fettell, N.A., Richards, R.A., 2008. Quantitative trait loci for water-soluble carbohydrates and associations with agronomic traits in wheat. Australian Journal of Agricultural Research 59, 891-905.

Reynolds, M.P., Delgado-B, M.I., Guiterrez-Rodriguesz, M., Larque-Saavedra, A., 2000. Photosynthesis of wheat in a warm, irrigated environment. I. Genetic diversity and crop productivity. Field Crops Research 66, 37-50.

Reynolds, M.P., Singh, R.P., Ibrahim, A., Ageeb, O.A.A., Larque-Saavedra, A., 1998. Evaluating physiological traits to complement empirical selection for wheat in warm environments. Euphytica 100, 85-94.

Robson, A.D., Pitman, M.G., 1983. Interactions between nutrients in higher plants. Encyclopedia of plant physiology. New Series. Volume 15A. Inorganic plant nutrition, 147-180.

Russell, G., Wilson, G.W., 1994. An Agri-Pedo-Climatological Knowledge-Base of Wheat in Europe. Joint Research Centre_European Commsion, Luxembourg.

Ruuska, S.A., Rebetzke, G.J., van Herwaarden, A.F., Richards, R.A., Fettell, N.A., Tabe, L., Jenkins, C.L.D., 2006. Genotypic variation in water-soluble carbohydrate accumulation in wheat. Functional Plant Biology 33, 799-809.

Saini, H.S., Aspinall, D., 1982. Sterility in wheat (*Triticum aestivum* L.) induced by water deficit or high temperature: possible mediation by abscisic acid. Australian Journal of Plant Physiology 9, 529-537.

Salvucci, M.E., Crafts-Brandner, S.J., 2004. Inhibition of photosynthesis by heat stress: the activation state of Rubisco as a limiting factor in photosynthesis (Review). Physiologia Plantarum 120 179–186.

Sattelmacher, B., Marschner, H., Kuhne, R., 1990. Effects of the temperature of the rooting zone on the growth and development of roots of potato (Solanum tuberosum). Annals of Botany 65, 27-36.

Savin, R., Nicolas, M.E., 1996. Effects of short periods of drought and high temperature on grain growth and starch accumulation of two malting barley cultivars. Australian Journal of Plant Physiology 23, 201-210.

Shpiler, L., Blum, A., 1986. Differential reaction of wheat cultivars to hot environments. Euphytica 35, 483-492.

Slafer, G.A., 1996. Differences in phasic development rate amongst wheat cultivars independent of responses to photoperiod and vernalization. A viewpoint of the intrinsic earliness hypothesis. Journal of Agricultural Science 126, 403-419.

Slafer, G.A., Rawson, H.M., 1994. Sensitivity of wheat phasic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. Australian Journal of Plant Physiology 21, 393-426.

Slafer, G.A., Savin, R., 1991. Developmental base temperature in different phenological phases of wheat (Triticum-aestivum). Journal of Experimental Botany 42, 1077-1082.

Snape, J.W., Butterworth, K., Whitechurch, E., Worland, A.J., 2001. Waiting for fine times: genetics of flowering time in wheat. Euphytica 119, 185-190.

Sofyan, A., Nurjaya, Kasno, A., 2004. Status hara tanah sawah untuk rekomendasi pemupukan (Nutrients status for recommendation of fertilisation). In: Agus, F., Abdimiharja, A., Harjowigeno, S., Fagi, A.M., Hartatik, W. (Eds.), Tanah sawah dan teknologi pengelolaannya (Rice field and management). Soil and Agroclimate Research Centre, Dept. Agriculture, Indonesia, Jakarta.

Stone, P., 2001. The effect of heat stress on cereal yield and quality. In: Basra, A.S. (Ed.), Crop responses and adaptations to temperature stress. The Howart, New York, pp. 243-292.

Stone, P.J., Nicolas, M.E., 1995. A survey of the effects of high-temperature during grain filling on yield and quality of 75 wheat cultivars. Australian Journal of Agricultural Research 46, 475-492.

Summerfield, R.J., Roberts, E.H., Ellis, R.H., Lawn, R.J., 1991. Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. Experimental Agriculture 27, 11-31.

Tahir, I.S.A., Nakata, N., Yamaguchi, T., Nakano, J., Ali, A.M., 2008. Influence of high shoot and root-zone temperatures on growth of three wheat genotypes during early vegetative stages. Journal of Agronomy and Crop Science 194, 141-151.

Tahir, I.S.A., Nakata, N., Yamaguchi, T., Nakano, J., Ali, A.M., 2009. Physiological response of three wheat cultivars to high shoot and root temperatures during early growth stages. Plant Production Science 12, 409-419.

Taiz, L., Zeiger, E., 2002. Plant Physiology. Sinaeur Associates, Inc., Publishers, Sunderland, Massachusetts.

Tashiro, T., Wardlaw, I.F., 1990. The response to high temperature shock and humidity changes prior to and during the early stages of grain development in wheat. Australian Journal of Plant Physiology 17, 551-561.

Tewolde, H., Fernandez, C.J., Erickson, C.A., 2006. Wheat cultivars adapted to post-heading high temperature stress. Journal of Agronomy and Crop Science 192, 111-120.

van Herwaarden, A.F., Angus, J.F., Richards, R.A., Farquhar, G.D., 1998. 'Haying-off', the negative grain yield response of dryland wheat to nitrogen fertiliser - II. Carbohydrate and protein dynamics. Australian Journal of Agricultural Research 49, 1083-1093.

Villareal, R.L., Klatt, A.R., 1985. Wheat for more tropical environments; A proceeding of International Symposium. CIMMYT, Mexico.

Wahid, A., Gelani, S., Ashraf, M., Foolad, M.R., 2007. Heat tolerance in plants: an overview. Environmental and Experimental Botany 61, 199-223.

Wall, P.C., 1987. Central and South America. In: Klatt, A.R. (Ed.), Wheat production constraints in tropical environments. CIMMYT, Mexico, pp. 27-36.

Wardlaw, I.F., 2002. Interaction between drought and chronic high temperature during kernel filling in wheat in a controlled environment. Annals of Botany 90, 469-476.

Wardlaw, I.F., Moncur, L., 1995. The response of wheat to high temperature following anthesis. I. The rate and duration of kernel filling. Australian Journal of Plant Physiology 22, 391-397.

Wardlaw, I.F., Sofield, I., Cartwright, P.M., 1980. Factors Limiting the Rate of Dry Matter Accumulation in the Grain of Wheat Grown at High Temperature. Functional Plant Biology 7, 387-400.

Watson, E.R. Lapins P. and Barron R. J. W., 1976. Effect of waterlogging on the growth, grain and straw yield of wheat, barley and oats. *Australian Journal of Experimental Agriculture and Animal Husbandry: 16, 114-122*

Watts, W.R., 1974. Leaf extension in Zea mays. 3. Field measurements of leaf extension in response to temperature and leaf water potential. Journal of Experimental Botany 25, 1085-1096.

Wheeler, T.M., Craufurd, P.Q., Ellis, R.H., Porter, J.R., Varaprad, P.V., 2000. Temperatur variability and the yield of annual crops. Agriculture Ecosystems and Environment 82, 159-167.

Wheeler, T.R., Hong, H.D., Ellis, R.H., Batts, G.R., Morison, J.I.L., Hadley, P., 1996a. The duration and rate of grain growth, and harvest index, of wheat (Triticum aestivum L) in response to temperature and CO2. Journal of Experimental Botany 47, 623-630.

Wheeler, T.R., Hong, T.D., Ellis, R.H., Batts, G.R., Morison, J.I.L., Hadley, P., 1996b. The duration and rate of grain growth, and harvest index, of wheat (Triticum aestivum L.) in response to temperature and CO 2. Journal of Experimental Botany 47, 623-630.

Whitechurch, E.M., Snape, J.W., 2003. Developmental responses to vernalization in wheat deletion lines for chromosomes 5A and 5D. Plant Breeding 122, 35-39.

Wiegand, C.L., Gerbermann, A.H., Cuellar, J.A., 1981. Development and yield of hard red winter wheats under semitropical conditions. Agronomy Journal 73, 29-37.

WMO, 2012. Weather Information for Lombok (http://worldweather.wmn.int/043/c00654.htm). World Meteorological Organisation.

Worland, A.J., 1996. The influence of flowering time genes on environmental adaptability in European wheats. Euphytica 89, 49-57.

Wuest, S.B., Cassman, K.G., 1992. Fertilizer-nitrogen use efficiency of irrigated wheat: I. Uptake efficiency of preplant versus late-season application. Agronomy Journal 84, 682-688.

Zhou, S., Ma, Y., Wang, C., Wang, H., Lu, F., 2000. Influence of drought stress on root growth and nutrient metabolism of winter wheat. Acta Agriculturae Boreali-Sinica 15, 57-62.

Zubaidi, A, McDonald, G. K. and Hollamby, G. J., 1999. Nutrient uptake and distribution by bread and durum wheat under drought conditions in South Australia. *Australian Journal of Experimental Agriculture,* 1999, **39**, 721–32

CHAPTER 3

DEVELOPMENT OF WHEAT UNDER CONTINUOUS HIGH TEMPERATURE IN A TROPICAL ENVIRONMENT

Akhmad Zubaidi[1,2], Gurjeet Gill[1] and Glenn K McDonald[1,3]

[1]School of Agriculture Food and Wine, The University of Adelaide

akhmad.zubaidi@adelaide.edu.au

gurjeet.gill@adelaide.edu.au

glenn.mcdonald@adelaide.edu.au

[2]Faculty of Agriculture, The University of Mataram, Indonesia

[3]Corresponding author

School of Agriculture Food and Wine,

The University of Adelaide

Waite Campus

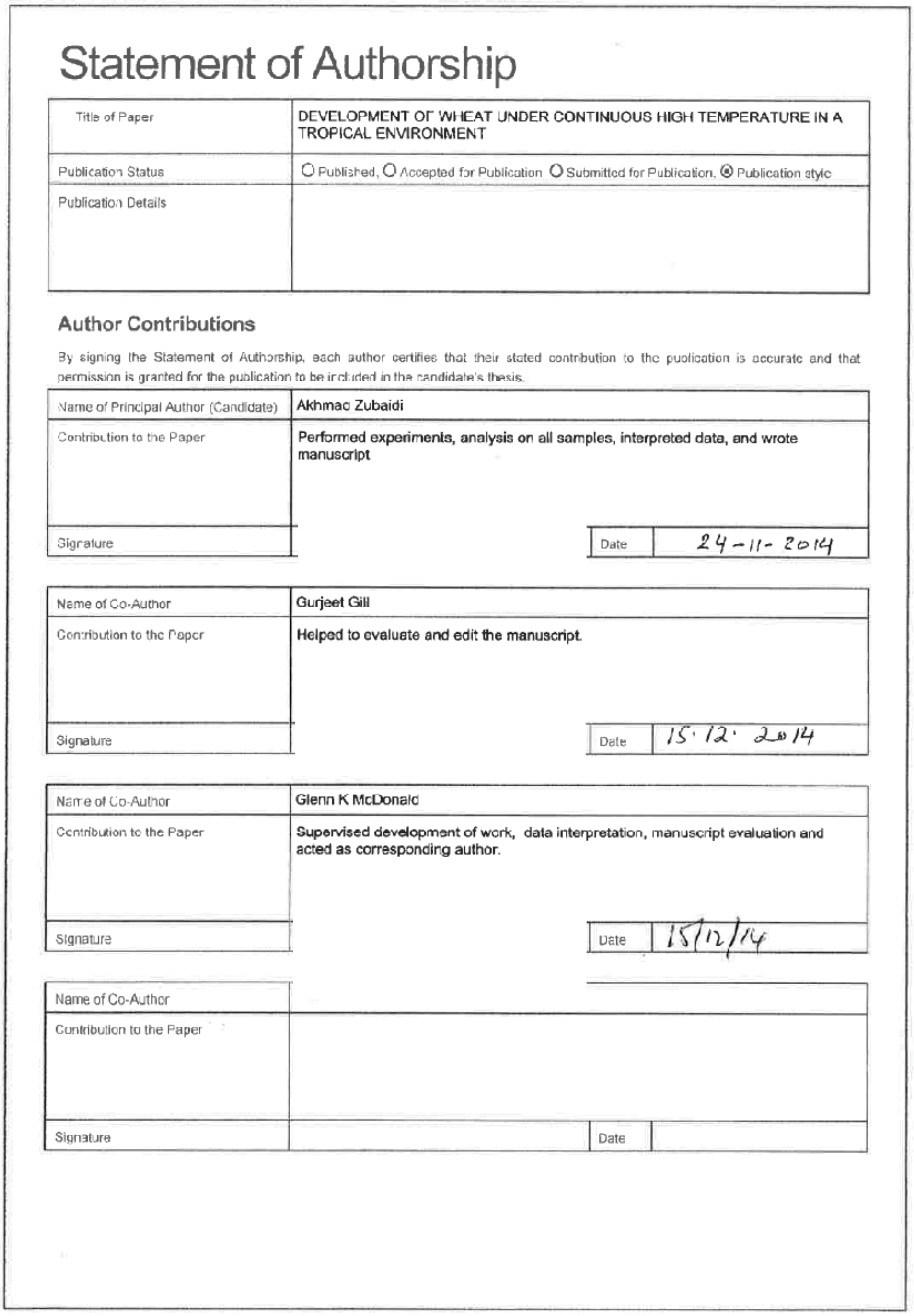
PMB 1 Glen Osmond, South Australia, 5054

AUSTRALIA

Email: glenn.mcdonald@adelaide.edu.au

Phone: +61 8 8303 7358

Word count:	7246
Line number:	397
Number of Table:	8
Number of figure:	4



Statement of Authorship

Title of Paper	DEVELOPMENT OF WHEAT UNDER CONTINUOUS HIGH TEMPERATURE IN A TROPICAL ENVIRONMENT
Publication Status	○ Published, ○ Accepted for Publication ○ Submitted for Publication, ● Publication style
Publication Details	

Author Contributions

By signing the Statement of Authorship, each author certifies that their stated contribution to the publication is accurate and that permission is granted for the publication to be included in the candidate's thesis.

Name of Principal Author (Candidate)	Akhmad Zubaidi		
Contribution to the Paper	Performed experiments, analysis on all samples, interpreted data, and wrote manuscript		
Signature		Date	24-11-2014

Name of Co-Author	Gurjeet Gill		
Contribution to the Paper	Helped to evaluate and edit the manuscript.		
Signature		Date	15.12.2014

Name of Co-Author	Glenn K McDonald		
Contribution to the Paper	Supervised development of work, data interpretation, manuscript evaluation and acted as corresponding author.		
Signature		Date	15/12/14

Name of Co-Author			
Contribution to the Paper			
Signature		Date	

ABSTRACT

Wheat production in tropical countries has increased substantially over the past 30 years to meet growing consumer demand and there is continued interest in tropical wheat production in many countries. Indonesia is the largest importer of wheat in South East Asia and *per capita* consumption is expected to increase. This, together with changes in climate in Indonesia may provide an opportunity for wheat to be produced as a dry season crop in rotation with rice. The feasibility of wheat production in parts of Indonesia as an alternative dry season crop is currently being investigated. Examining the importance of crop maturity and its interaction with time of sowing is important to evaluate plant adaptation

Experiments were conducted under controlled conditions and in the field on Lombok Island, Indonesia to examine the patterns of development of wheat under high temperatures. Varieties of spring wheat representing a range of maturity types were grown at 30/23°C day/night temperatures with 12 hours photoperiod. These conditions mimicked the field growing environment on Lombok. A field experiment with 10 varieties sown at 6 times (mid April to late June) was also conducted on Lombok Island Indonesia in 2010 at low (Gunung Sari) and high (Sembalun) elevations. Mean growing season temperatures varied by about 5°C (27°C vs 22°C) between the two sites. The varieties used in this study were selected to represent different alleles at specific photoperiod (Ppd-1D) and vernalisation (Vrn-1A, Vrn-1B and Vrn-1D) loci.

The rates of development observed in the growth room and in the field experiments were similar. Plant development was rapid under this high temperature environment with flowering occurring 40-70 days after sowing in most varieties. Leaf appearance rates did not differ and spikelet number per head showed a small difference among the varieties. Differences in flowering among the varieties were related mainly to photoperiod sensitivity although there was some evidence that intrinsic earliness was also influential. Time to flower at the cooler site at Sembalun and the warmer site at Gunung Sari were similar, with the exception of Yitpi, which showed considerable delay in flowering at Gunung Sari. At Sembalun time to flower did not vary consistently with sowing date, but at the Gunung Sari early sowing delayed flowering by 10 to 30 days. While temperatures were higher at the early sowing dates, they only differed by 1-2°C and this was not considered high enough to induce such a large delay in flowering. Despite variation in the phasic development among varieties, the number of grains per spikelet and grain yield per plant was not associated with the differences in phasic development. While manipulating the timing of important developmental stages will be important in the timing of flowering, it did not appear to have a direct influence in the yield potential of a variety. Consistency in time to flower across wheat genotypes (except Yitpi) and planting dates could be an important finding for the adaptation of wheat to tropical environments. It should now be possible to select planting time of wheat to allow the maturity and harvest of the crop to coincide with the driest time of the year.

1. INTRODUCTION

Production of wheat in tropical countries is small but it has increased substantially reflecting the growing demand for wheat-based products in these regions. Current production in tropical countries (excluding India, Pakistan and Mexico) is about 14Mt, but it has increased seven-fold since the 1960s (FAO, 2012). Countries in South East Asia import large amounts of wheat for domestic consumption and processing and this has increased considerably with economic development. In 1960 South East Asian countries imported about 1 Mt wheat which increased to about 9 Mt in the 2000s (FAO, 2012). Indonesia is the largest single importer of wheat in the region with an estimated 7.4 Mt of grain imported in 2012 (Siregar, 2012).

Average consumption of wheat in Indonesia is 21.5 kg/person/year, which is lower than average world consumption (65.9 kg/person/year) but it is steadily increasing (FAO, 2012). There is no commercial wheat production in Indonesia but there is some interest in investigating the feasibility of local production in response to rising domestic demand for wheat and to help improve food security. Some local production would help to lower the high cost of the subsidy for imported wheat grains. It has also been suggested that the predicted effects of climate change on Indonesian agriculture may influence changes in cropping practices which may provide an opportunity for wheat production. With a change in climate it is likely that the wet season in parts of Indonesia will become shorter and more intense and the dry season longer. While rice will remain the dominant cereal crop, it is recognised that there will need to be some diversification of the cropping systems to adapt to the predicted changes in climate (Kardono et al. 2012). A review of technological changes and investment required to maintain food security in the face of climate change identified tropical wheat as an opportunity (Kardono et al 2012). Consequently, the Indonesian Department of Agriculture is aimed for some commercial production of wheat by 2014 (Medan-Bisnis, 2012). Potentially, wheat could grow during the dry season as it is more drought tolerant than rice. However, improved adaptation of wheat to tropical environments is needed to achieve this goal. Initial evaluation of wheat varieties introduced from India (which subsequently were released as the Indonesian varieties Nias, Dewata, and Selayar) in the highlands of Java island showed that grain yields of 2.7–5.7 t/ha could be produced (Handoko, 2007) but wheat cultivation was only practised under experimental conditions. Simulation model by Gusmayanti et al. (2006) and Handoko (2007) also showed wheat could be potentially grown in Indonesia and that yields of between 1.5-3.0 t/ha could be achieved.

Lombok Island in Indonesia (8.5°S 116.3°E) has a hot and humid environment with distinct wet and dry seasons. The wet season extends from October to April with 1295 mm of rainfall being received (monthly average 215 mm) while the dry season lasts from May to September when only 219 mm is received (monthly average 36 mm). At Mataram, which is on the coast, the average maximum temperature is 30.9^{o}C during the day and the minimum temperature is 22°C at night (WMO, 2012) (http://worldweather.wmo.int/043/c00654.htm) (Figure 3.1), although these temperatures are moderated by the high elevation in the centre of the island. Mt. Rinjani, the highest mountain on the island, has an elevation of 3,700m which allows temperate fruits and vegetables to be grown, but temperatures exceeding 25°C are still common. These temperatures are much higher than those experienced during seedling development in many other regions of the world where wheat is grown. Seasonal variation in daylength is small with an annual variation of about 1 hour but only 0.3 hour during the dry season (Fig 3.1). The growing environment on the island is therefore characterised by consistently high temperatures and constant daylength.

Wheat is a winter cereal that evolved in temperate environments, but this may not preclude high yields being achieved under hotter conditions. Under controlled conditions, Rawson (1988)demonstrated that high yields are achievable by some genotypes when wheat was grown at 30/25°C and there is considerable genetic variation in tolerance to high temperatures, but he emphasised the importance of growth during the early phases of crop development to achieving high yields. Rates of early development increase up to an optimum of around 20°C, after which development rate slows or decline (Slafer and Rawson 1995a,b). This optimum is considerably lower than the temperatures experienced in tropical regions, but as development proceeds to flowering the optimum and base temperatures for development increase. The high temperatures at sowing in tropical environments can mean that wheat may establish poorly (Fischer, 1985) and early development can be rapid which shortens the growing period and leads to reduced growth and yield (Fischer, 1985; Rawson, 1988b). Together with rapid vegetative and reproductive development, grain number and individual grain weight can be low (Bagga and Rawson, 1977; Warrington et al., 1977; Midmore et al., 1982; Fischer, 1985). If the time from seeding to flowering could be made longer, wheat could potentially have a higher biomass production which may lead to greater yields (Fischer, 1985), although Midmore et al. (1982) found that this may not always be effective.

Characterising the development of wheat and the importance of difference developmental controls of flowering is important to help find varieties adapted to tropical conditions.

The environment strongly influences the physiological mechanisms that trigger the transition of phases in crop development and understanding how varieties respond to these development cues in tropical environments will assist with the development of adapted varieties. Temperature and photoperiod are among the environment components that most affect plant growth and development (Slafer and Rawson, 1994; Snape et al., 2001). At low latitudes variation in daylength is small and a variety's sensitivity to the seasonal changes in daylength and its response to supra-optimal temperatures during the early stages of development may be an important adaptive characteristic. In hot environments, sowing time and elevation are important ways of altering exposure to high temperatures (Midmore et al. 1982) although the response also depends on a variety's sensitivity to temperature and daylength. Inherent earliness is another characteristic controlling wheat development, which is independent of photoperiod and vernalisation (Slafer, 1996; Appendino and Slafer, 2003) and could influence development in tropical environments. Midmore et al. (1982) suggested that having a vernalisation requirment may also be useful to delay development in tropical environments.There is considerable variation in maturity among Australian wheat varieties that is associated with combinations of photoperiod and vernalisation responsiveness (Eagles et al. 2009, 2010). The development of diagnostic molecular markers for important photoperiod and vernalisation genes has allowed their importance to heading across the Australian cereal zone to be analysed. A similar approach would help improve understanding of adaptation of wheat in tropical regions.

Prediction of phasic development is essential for evaluating cultivar adaptation and scheduling for cultural practice (Shaykewich, 1995). Investigation of high temperature effects on wheat growth and development has often focussed on later development phases such as from flowering to maturity because heat stress generally occurs later in the growing season in many of the important wheat production regions. The effect of temperature and photoperiod on the phasic development of wheat are widely published, however, in most cases experiments to examine the effects of high temperature have used cooler conditions than those experienced in tropical regions such as Lombok. In one of the few studies on development at high temperatures, Rawson (1988a) found only small differences in ear initiation and ear development when they were grown at 30/25°C. The aim of this work is to describe the pattern of apical development of wheat varieties with different developmental genes, under continuous high temperature in order to investigate wheat production in a tropical environment. Initially a small number of Australian spring varieties spanning a range of maturities were grown at high temperatures to document the level of variation among varieties wheat commonly used in the main cereal zone in Australia. The second part of the work examined development in the field on Lombok Island over a number of sowing dates to examine the sensitivity to sowing time and elevation among 10 varieties of spring wheat. The aim of the field work was to verify the responses observed in the growth room in the target environment and to assess the potential impact of important developmental genes on flowering time in a tropical environment.

2. MATERIALS AND METHODS

Experiments were conducted in a growth room in Adelaide and at 2 locations on Lombok Island, Indonesia.

2.1. Growth room experiments

A high temperature treatment was imposed in the growth room on 4 Australian wheat cultivars, Axe, Gladius, Janz and Yitpi. Plants were grown at 32°/23°C under a 12 hour photoperiod, imitating the temperature and day length of tropical areas of Lombok Island, Indonesia (Figure 3.1). This temperature regime was maintained throughout the experiments

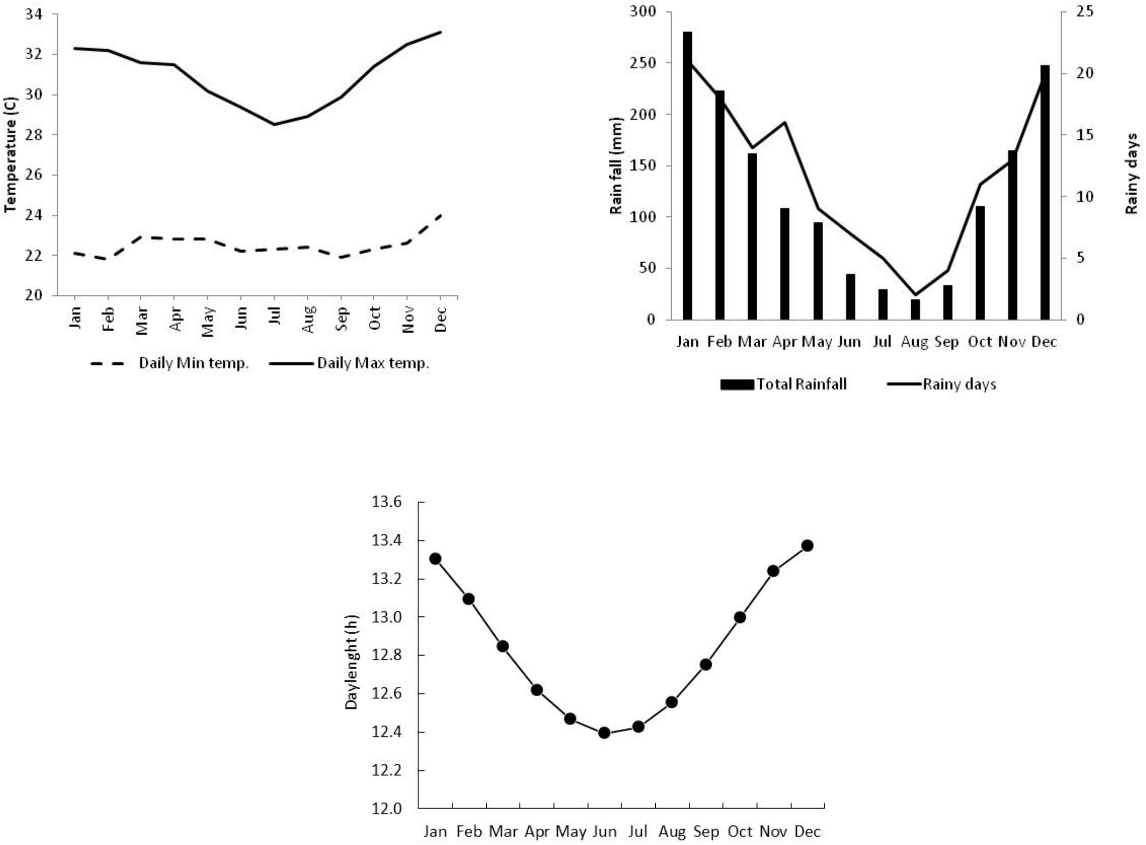


Figure 3.1: Long term average of daily maximum and minimum temperature (left) and total rainfall and rainy days and average daylength (plus civil twilight) for Mataram on Lombok Island. [Sources: rainfall and temperature World Meteorological Organisation (http://worldweather.wmo.int/043/c00654.htm); daylength: US Naval Observatory (http://aa.usno.navy.mil/data/)]

Table 3.1: The genotype of the Australian varieties for the Ppd-1 and Vrn-1 genes (Eagles et al., 2009) and the responsiveness to photoperiod, vernalisation and the basic vegetative phase (Brougham, 2006)[A]. Spring allele: a,b; winter allele: v

Var.	Ppd-D1	Vrn-A1	Vrn-B1	Vrn-D1	BVP	Ppd	Vern
Axe	a	a	a	v	910[B]	525	0
Silverstar	a	a	a	a	-	-	-
Mira	a	a	a	v	-	-	-
Gladius	b	a	a	v	910	917	0
Hartog	a	v	a	a	882	549	182
Janz	a	a	v	v	906	776	0
Sunvale	a	a	v	a	1323	973	0
Yitpi	b	a	a	v	1176	1973	0

[A] Plants were grown in a growth room at 21°C either under an 8 hour or 18 hour photoperiod. Imbibed seeds were maintained at 4-6°C for 6 weeks to vernalise the plants. The vernalisation response was assessed as the difference in the time to ear initiation between vernalised and non-vernalised plants under long days. Photoperiod response was assessed as the difference in ear emergence of vernalised plants under long and short photoperiods and the BVP was measured as the time to ear emergence of vernalised plants grown under long photoperiod.

[B] number shows the thermal time requirement to fulfil BVP, photoperiod or vernalisation

The varieties used were Axe, Gladius, Janz and Yitpi which represent a range of maturity types among Australian varieties with Axe being the earliest to flower and Yitpi the latest. The varieties differ mainly in their sensitivity of photoperiod with Axe and Janz possessing the insensitive allele (*Ppd-D1a*) and Gladius and Yitpi possessing the sensitive allele (*Ppd-D1b*) (Eagles *et al.* 2009). These genes are important to flowering time among Australian wheat varieties although they do not explain all the observed variation in flowering (Eagles et al. 2010). The response to vernalisation and photoperiod of these varieties at a lower temperature has also been described by Brougham (2006) (Table 3.1).

There were 2 consecutive experiments. In the first experiment, seeds were sown on February 13, 2010, in small pots of 5 cm diameter and 8.4 cm depth filled with a commercial potting mix. One plant was grown in each pot. The pots were arranged in 12 trays, each tray containing 24 pots consisting of 6 replicate pots of the 4 varieties. Plants were watered daily throughout the experiment. Two trays were harvested at 5 times for apical dissections with the final harvest occurring at 50 days after sowing. The number of fully emerged leaves was counted at weekly intervals to estimate rates of leaf appearance. Harvests were made at 3-5 day intervals. By the final harvest Axe had flowered (Z69; Zadoks et al. 1977), the flag leaf was emerging in Gladius and Janz (Z40-45) and Yitpi had commenced stem elongation (Z32). At each harvest observations were made on 6 plants from each of the two replicates. The experiment was designed as a randomised complete block.

Bigger pots of 25 cm diameter were used in the second growth room experiment to allow plants to grow to maturity. The four varieties used in the previous experiment, Axe, Gladius, Janz and Yitpi, were sown on March 26, 2010 in pots each with 8 plants, with 6 replications. The plants were thinned after emergence leaving 5 plants/pot. Observations on the number of fully emerged leaves were made at approximately weekly intervals. Six plants were harvested at 3 to 4 days intervals for apical dissection. Sampling commenced first in Axe, as it had shown quickest development in the first experiment, then Gladius and Janz, while sampling of Yitpi commenced last. Sampling and apical dissection continued until terminal spikelet initiation occurred at which time one or two plants were left in each pot to measure time to flowering.

Apical measurements

The main stem of each plant was dissected and the shoot apex was observed under a binocular dissecting microscope for stage of development and to record time of double ridge stage, terminal spikelet initiation (TSI), and the number of spikelet primordia. Dissections were repeated 5 times throughout plant growth in both experiments. During dissections, number of leaves (Haun, 1973) and plant development stages (Zadoks et al., 1977) were also recorded.

2.2. Field experiments

A field experiment was conducted on Lombok, Indonesia (8.5°S 116.3°E) in 2010 to examine crop responses to time of sowing. The experiment was designed with 6 sowing dates at 2 different sites, Gunung Sari and Sembalun which differed in elevation (Table 3.2). The field experiments were conducted in farmers' fields and the experiment at Gunung Sari followed a rice crop, while at Sembalun the experiment was sown after mixed cropping of capsicum and strawberry. Two Indonesian varieties originally introduced from India, Nias and Dewata, were included in the field experiment in addition to 8 Australian wheat cultivars, Axe, Silverstar, Mira, Gladius, Hartog, Janz, Sunvale and Yitpi (Table 3.1). These varieties were selected to have different combinations of alleles at Vrn1 and Ppd1 based on information published by Eagles et al (2009) in order to examine the effects of these developmental genes on the phasic development of the varieties over a range of sowing times at the two sites. Air temperatures at the sites were monitored using Tiny Tag® data logger (Gemini Data Loggers), while rainfall data were obtained from nearby weather stations.

Each variety was sown in plots of 3, 1 m-long rows. Compound fertilizer N-P-K (Phonska 15-15-15) was apply at sowing time at a rate of 300 kg/ha, and nitrogen fertilizer (Urea, 45% N) was apply 3 times at sowing time, tillering and heading, with rate 300 kg Urea/ha. No biocide was applied during plant growth.

It was considered that it was important to characterise the responses to time of sowing by using sowing times that spanned the maximum range in dates in the limited space available at both sites. An additional constraint was the limited amount of seed available for some varieties. Therefore the plots at each site were non-replicated.

Table 3.2: Site name, altitude, average temperature measured during the experiment and rainfall on sites and sowing date of field experiment

	Site	
	Guning Sari	Sembalum
Altitude (m asl)	50	1000
Temperature (Max-Min) (°C)	32.0-23.1	27.3-15.7
Rainfall (mm)[A]	958	409
Sowing dates		
1	17 April	19 April
2	1 May	3 May
3	15 May	17 May
4	29 May	31 May
5	12 June	15 June
6	26 June	28 June

[A] Rain fall of 5 month during experiment (compared with long term average during the same period; 294 mm)

plastic bag and transported to the laboratory at the University of Mataram. The apex on the main stem was examined to determine the time of double ridge appearance, terminal spikelet initiation, apex length and spikelet primordia number.

Yield and yield components

At maturity 10 plants per plot were harvested and grain yield and the yield components ears/plant, spikelets/ear, grains/spikelet and kernel weight were estimated on each plant.

Data analysis

Data were analysed using Genstat (11th edition). Data from each growth room experiment were analysed by ANOVA. Leaf appearance rates and phyllochron in the growth room and field experiments were quantified using linear regressions with differences among genotypes assessed using the 95% confidence interval of the slope. Data from the field trials are presented as mean± standard error of mean (s.e.m.) and Student's t-test was used to assess the differences between the mean values.

3 RESULTS

3.1 Growth room Experiment

3.1.1. Rate of leaf appearance

Axe had the fastest rate of leaf appearance (0.23-0.25 leaves/d) while there was no significant difference in the rate of leaf appearance among the remaining varieties (0.135-0.177 leaves/d; Table 3.3). The phyllochron for Axe (3.9-4.4 d; equivalent to 107-121°Cd) was significantly shorter than the other varieties (5.5-7.0 d; equivalent to 151-193°Cd).

3.1.2. Apical development

The timing of key stages of apical development was similar in both growth room experiments. Double ridge appearance was observed after 17 days in Axe, followed by Gladius and Janz (approximately 25 days) and Yitpi took 35 days to reach double ridge. A similar difference among the varieties was seen in the time to terminal spikelet initiation and the duration of the spikelet initiation phase. In all cases the length of the growth phase in Yitpi was about twice that of Axe, with Gladius and Janz being intermediate. In the second experiment the time from terminal spikelet initiation to flowering was 47 days in Yitpi but was only 20 days in the other varieties (Tables 3.4, 3.5).Axe flowered 40-46 days after sowing followed by Gladius and Janz (52-59 days), and Yitpi was the last to flower (92-97 days; Table 3.5).

Among the four varieties Axe and Janz possessed the photoperiod insensitive allele *Ppd-D1a*and Gladius and Yitpi possessed the photoperiod sensitive allele *Ppd-D1b*. At-test was used to assess the influence of these alleles on development in this experiment. The presence of *Ppd-D1a* advanced the time to double ridge by about 10 days (21.1 *vs* 32.2, s.e.d.= 3.03, $P<0.01$ and 19.7 *vs* 28.0, s.e.d.= 2.57, $P<$ 0.01in experiments 1 and 2 respectively) and terminal spikelet initiation by a similar amount (29.3 *vs* 41.0 s.e.d.= 3.78 $P<0.01$ and 25.0 *vs* 38.6, s.e.d. = 3.75, $P=0.001$in experiments 1 and 2 respectively). However Yitpi developed more slowly compared to Gladius despite having the same Ppd-D1 and Vrn-1 alleles. Although there were significant differences among varieties in the time taken to reach the double ridge, terminal spikelet initiation and the duration of the spikelet initiation phase, the total number of spikelet primordia initiated did not differ significantly among the varieties because of variation in the rates of spikelet initiation compensated for differences in duration of the spikelet development phase. For example, the rate of spikelet initiation in Axe was more than twice that of Yitpi but it had a much shorter spikelet initiation phase (Table 3.4).

3.2. Field Experiment

Higher than average rainfall was received in 2010; the monthly rainfall during the experiment was 3-10 times higher than the long-term average. Water logging occurred at Gunung Sari at the first three sowing times which resulted in slow and poor crop establishment.

3.2.1. Rates of leaf appearance

Leaf appearance rates and phyllochron did not differ significantly among the varieties at either site (Table 3.3). The mean rate of leaf appearance at Gunung Sari (0.176 leaves/day) was lower than at Sembalun (0.202 leaves/day) and the corresponding phyllochron was slightly longer (5.4 *cf* 4.9 days/leaf). The two Indonesian varieties, Nias and Dewata, showed similar rates of leaf appearance as the Australian varieties. The rates of leaf appearance in the two field experiments are comparable to those measured in the growth room, with the

Table 3.3: Average rates of leaf appearance (leaves/day) and the phyllochron (days/leaf) for bread wheat varieties grown in growth room at 30°C/23°C (day/night) and 12 h photoperiod and in two field experiments. The upper and lower limits of the 95% confidence interval are shown in parentheses.

Variety	Growth Room 1	Growth Room 2	Gunung Sari	Sembalun
		(a) Leaf appearance		
Axe	0.23 (0.22, 0.24)	0.25 (0.23, 0.28)	0.19 (0.14, 0.24)	0.19 (0.14, 0.24)
Gladius	0.18 (0.16, 0.20)	0.17 (0.13, 0.22)	0.15 (0.12, 0.19)	0.18 (0.15, 0.21)
Janz	0.18 (0.15, 0.21)	0.14 (0.09, 0.19)	0.17 (0.15, 0.20)	0.22 (0.19, 0.26)
Yitpi	0.17 (0.15, 0.19)	0.14 (0.09, 0.18)	0.20 (0.16, 0.24)	0.20 (0.18, 0.21)
Nias	-	-	0.16 (0.14, 0.19)	0.22 (0.21, 0.24)
Dewata	-	-	0.17 (0.10, 0.24)	0.20 (0.18, 0.22)
		(b) Phyllochron		
Axe	4.4 (4.2, 4.5)	3.9 (3.6, 4.3)	4.8 (3.5, 6.1)	5.1 (3.7, 6.5)
Gladius	5.6 (4.9, 6.3)	5.6 (4.2, 7.1)	6.2 (4.9, 7.5)	5.5 (4.6, 6.4)
Janz	5.5 (4.6, 6.5)	6.5 (4.4, 8.9)	5.6 (4.9, 6.4)	4.5 (3.8, 5.1)
Yitpi	5.8 (5.2, 6.8)	7.0 (4.7, 9.4)	4.8 (3.9, 4.7)	5.1 (4.7, 5.5)
Nias			5.9 (4.8, 6.9)	4.5 (4.2, 4.8)
Dewata			4.9 (2.9, 7.0)	5.1 (4.6, 5.5)

Table 3.4: Time to double ridge, terminal spikelet initiation, length spikelets phase, spikelet number at terminal spikelet initiation and length, and rate of spikelet initiation in growth room experiments (GR1 and GR2)

Varieties	Double ridge (DAS)		Terminal spikelet initiation (DAS)		Spikelet initiation duration (days)		Spikelets per spike		Rate of spikelet initiation (day^{-1})	
	GR1	GR2	GR1	GR2	GR1	GR2	GR1	GR2	GR1	GR2
Axe	17.0	17.0	22.6	21.2	5.6	4.2	12.6	13.6	2.3	3.3
Gladius	25.2	22.3	31.1	30.7	5.9	8.4	14.2	13.0	1.7	1.6
Janz	26.1	23.6	34.6	32.0	8.5	8.4	14.2	13.4	2.4	1.2
Yitpi	39.2	32.5	48.8	45.4	9.6	12.9	12.0	13.8	1.3	1.1
mean	26.9	23.8	34.3	32.3	7.4	8.5	13.3	13.5	-	-
l.s.d	3.19	2.33	2.28	3.02	-	-	-	-	-	-

Table 3.5: Time to flower (days after sowing) in the growth room and field experiments. Values in the field are shown as the mean ± s.e.m

Variety	Growth Room 2	Gunung Sari	Sembalun
Axe	41	44 ± 3.3	50 ± 1.2
Silverstar	-	51 ± 1.9	53 ± 1.9
Mira	-	57 ± 2.2	56 ± 1.9
Gladius	52	59 ± 3.0	59 ± 0.9
Hartog	-	62 ± 2.4	58 ± 2.1
Janz	52	59 ± 2.0	62 ± 2.6
Sunvale	-	64 ± 2.7	69 ± 0.9
Yitpi	92	98 ± 6.2	80 ± 1.0
Nias	-	53 ± 3.1	53 ± 2.3
Dewata	-	66 ± 3.4	65 ± 2.2
Mean	59	61	61

exception of Yitpi and Axe, which had a slower rate of leaf appearance in the field (Table 3.3).

3.2.2. Apical development

The timing of apical development in both field experiments was similar. Axe showed the fastest development followed by Silverstar, Mira and Gladius, then Janz, Hartog and Sunvale, while Yitpi was the slowest in apical development (Table 3.6). Of the two Indonesia cultivars, Nias was earlier than Dewata, and showed a similar pattern as Mira and Gladius while Dewata was similar to Janz and Hartog. Dewata initiated slightly more spikelets (18-19 spikelets) than the other cultivars (12-16 spikelets). The number of spikelets initiated and the mean rates of spikelet initiation were the same at both sites (Table 3.6).

3.2.3. Time to flower

There was no significant difference in the mean time to flower between the two sites among the varieties with the exception of Yitpi, which flowered 18 days earlier at Sembalun. Axe,

Table 3.6: Time of double ridge, terminal spikelets, length spikelets phase, spikelet number at terminal spikelet initiation and length, and rate of spikelet formation in Gunung Sari (GS) and Sembalun (S). Values are shown as mean ± s.e.m. (N=5)

Varieties	Double Ridge (DAS)		Terminal spikelets (DAS)		Spikelet phase (days)		Spikelets number		Rate of spikelets initiation (day^{-1})	
	GS	S	GS	S	GS	S	GS	S	GS	S
Axe	18.0±1.22	16.3±0.75	23.4±1.47	22.0±1.00	5.4	5.7	12.0±0.41	13.8±0.48	2.2	2.4
Silverstar	21.0±0.00	21.0±0.00	29.0±1.00	29.0±1.00	8.0	8.0	14.8±0.48	12.0±0.91	1.9	1.5
Mira	21.0±0.00	24.0±2.00	29.8±1.18	29.3±0.67	8.8	5.3	17.3±1.25	17.0±0.91	2.0	3.2
Gladius	24.7±0.33	20.0±0.00	30.7±0.67	33.3±1.75	6.0	13.3	14.0±0.41	11.8±1.70	2.3	0.9
Hartog	28.0±0.0	29.3±0.67	37.7±3.71	36.5±3.50	9.7	7.2	12.0±5.00	16.5±0.50	1.2	2.3
Janz	28.0±0.00	29.8±1.75	34.3±0.75	36.8±1.75	6.3	7.0	15.3±2.59	12.8±2.21	2.4	1.8
Sunvale	32.0±1.53	27.3±0.67	40.7±2.96	43.0±1.00	8.7	15.7	13.2±0.86	12.0±2.80	1.5	0.8
Yitpi	35.0±2.04	31.5±2.02	41.3±3.50	45.5±2.02	6.3	14.0	14.0±0.71	16.3±0.95	2.2	1.2
Nias	20.2±0.49	22.8±0.75	30.0±0.00	31.3±1.25	9.8	8.5	15.8±2.50	16.0±1.53	1.6	1.9
Dewata	25.5±0.87	28.0±0.00	34.3±0.75	35.0±0.00	8.8	7.0	18.3±0.33	18.7±6.36	2.1	2.7
Mean	25.3	25.0	33.1	34.2	7.8	9.2	14.7	14.7	1.9	1.9

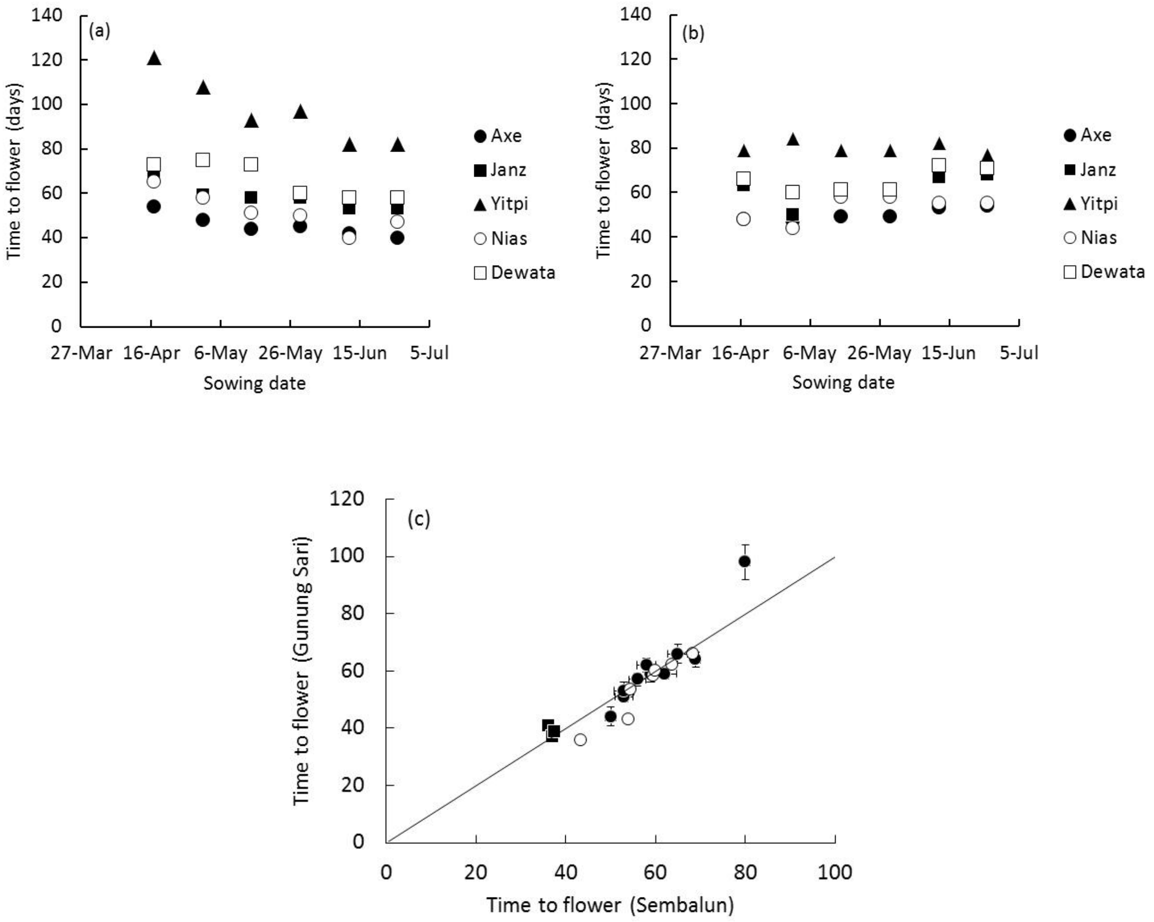


Figure 3.2: Flowering time of wheat varieties for each sowing datesat (a) Gunung Sari and (b) Sembalun for Axe, Janz, Yitpi, Nias and Dewata. These varieties represent the range in flowering times among the varieties. (c) The relationship between the mean time to flower at Gunung Sari and Sembalun based on all six sowing times (●).The error bars are the standard errors of the mean among the varieties and the 1:1 line is also shown. The mean temperatures before flowering were 27°C at Gunung Sariand 22°C at Sembalun. Data from Slafer and Rawson (1995a) (■) comparing mean temperatures of 22°C and 25°C under long days and Rahman and Wilson 1978 (○) comparing mean temperatures of 19.5°C and 27.5°C are also shown.

Silverstar and Nias developed fastest, flowering 46-53 days after sowing, followed by Mira, Gladius, Hartog, Janz, Dewata and Sunvale, while Yitpi showed the slowest development. The times recorded in the field were similar to those measured in the growth room (Table 3.5).

The response to sowing time differed between the two sites. Figure 3.2 shows the response to sowing date among Yitpi, Janz, Nias, Dewata and Axe, which represent the range of maturity types among the varieties. At Gunung Sari flowering was later in all varieties at the earliest sowing dates and especially with Yitpi which showed a 40 day difference in time to flower among the sowing dates (Fig 3.2a) whereas at Sembalun, time to flower varied little among the sowing dates (Fig 3.2b). Mean time to flower between the two sites did not differ

for most of the varieties (Fig 3.2c), but Yitpi showed the greatest sensitivity to temperature and a considerable delay in flowering at the warmer site. This was largely associated with the delay at the three earliest sowing dates at Gunung Sari but even when these sowing dates were excluded Yitpi showed a greater sensitivity to high temperature than the other varieties. The comparison between the two sites on Lombok showed a similar response to temperature in the earlier studies of Rahman and Wilson (1978) and Slafer and Rawson (1995a) that used comparable high temperatures under controlled conditions.

3.3. Effects of vernalisation, photoperiod and BVP

Varieties that have the allele which is sensitive to photoperiod (*PpD1-b*) showed significant delays in the time to flowering at both sites (Table 3.7). Time to terminal spikelet initiation was also shorter in varieties with the insensitive allele at Sembalun. The presence of the winter allele at Vrn-A1 delayed flowering at Gunung Sari while the winter allele at Vrn-B1 delayed flowering at Gunung Sari and terminal spikelet formation at

Table 3.7: Effect of photoperiod and vernalisation alleles on the time (days) to double ridge, terminal spikelet initiation and flowering at Gunung Sari and Sembalun. Data are from the 5th sowing date at Gunung Sari and the 4th sowing date at Sembalun. Means were compared by t-test and differences significantly ($P < 0.05$) different from zero are indicated (*)

Allele	Site					
	Gunung Sari			Sembalun		
	Double ridge	Terminal spikelet	Flowering	Double ridge	Terminal spikelet	Flowering
			PpD1			
a	23.9	31.9	52.8	26.5	32.1	57.0
b	27.7	36.7	68.9	29.3	39.4	68.9
Difference	-3.8	-4.9	-11.1	-2.8	-7.3	-11.9
s.e.d.	2.94	3.16	3.81*	3.72	3.10*	3.61*
			Vrn-A1			
a	24.7	32.5	55.0	26.1	34.0	60.0
v	28.0	37.7	59.6	28.7	36.5	59.8
Difference	-3.3	-5.2	-4.6	-2.7	-2.5	0.2
s.e.d.	4.61	4.49	2.24*	1.97	5.98	4.32
			Vrn-B1			
a	22.8	31.8	53.7	26.1	32.4	59.2
v	29.7	37.0	61.0	28.7	39.4	62.5
Difference	-6.9	-5.3	-7.3	-2.6	-7.0	-3.3
s.e.d.	1.86*	3.13	2.33*	1.97	3.29*	2.32
			Vrn-D1			
a	26.7	36.6	53.9	27.3	35.3	59.0
v	28.1	31.6	56.6	26.7	33.6	60.6
Difference	-2.6	5.0	-2.7	0.6	1.7	-1.6
s.e.d.	2.85	3.01	3.74	2.74	3.29	2.94

Sembalun. The winter alleles at Vrn-D1 did not significantly influence development (Table 3.7).

The other factor influencing development is the intrinsic earliness of the variety which is estimated as the BVP (Table 3.1). Brougham (2006) estimated the median value among the six varieties to be 910°Cd and the time to flower for the varieties with a BVP equal to or below the median (Axe, Gladius, Hartog and Janz) and above the median (Sunvale and Yitpi) were compared. A longer BVP was associated with significantly later flowering at Gunung Sari whether using all six sowing times (81.3 vs 55.9, s.e.d. = 6.23, $P = 0.001$) or after excluding the first three sowing dates (74.0 vs 52.7 s.e.d. = 6.10, $P < 0.001$) and a similar difference was observed at Sembalun (74.5 vs 57.3 s.e.d. 2.17, $P < 0.001$).

3.4. Relationships with yield per plant

Partial correlations were used to examine the influence of development on the yield per plant and its components. Partial linear correlations, rather than simple linear correlations were used to account for covariance among the traits. At the sowing times at which apical development was assessed, variation in grain yield per plant among the varieties at Gunung Sari (sowing 5) and at Sembalun (sowing 4) was associated with ears per plant (Gunung Sari: r = 0.82, $P<0.05$; Sembalun: r = 0.78, $P< 0.05$), grains/spikelet (Gunung Sari: r = 0.93, $P<0.01$; Sembalun: r = 0.88, $P <0.01$) but not with kernel weight (Gunung Sari: r = 0.73, n.s.; Sembalun: r = 0.64, n.s.). There was no significant correlation between yields and time to flower at either site (Gunung Sari: r = 0.57n.s.; Sembalun: r = 0.55, n.s.). The timing of double ridge and terminal spikelet initiation had little influence on yield and were not significantly correlated with yield per plant or any of the yield components.

4 DISCUSSION

An aim of this work was to examine patterns of development of wheat genotypes under continuous high temperature associated with a tropical environment. While the responses of wheat to changes in temperature and photoperiod have been studied extensively, much of the previous work on the effect of temperatures on development in wheat has been conducted at lower temperatures, typically 10-25°C, and/or over short periods of time (Rahman et al., 1977; Rawson, 1993; Rawson and Zajac, 1993; Ishag and Mohamed, 1996; Savin and Nicolas, 1996). Studies of the effects of higher and supra-optimal temperatures during early stages of development are less common. The early phases of apical development and leaf appearance have an optimum temperature of about 20°C (Slafer and Rawson 1995a,b), which was exceeded at the two experimental field sites (Fig3.1). Therefore, even at high elevations on Lombok, early development will occur at temperatures higher than the optima for vegetative and spikelet development. Sensitivity to temperature may therefore be an important adaptive trait for wheat production during the dry season. The initial studies on phenological development were conducted under controlled conditions to simulate the environment of the lowlands on Lombok Island and there was good agreement in the timing of different stages of development with the field studies. There are few studies that have compared controlled environment and field responses directly, but the data from this study suggest the growth room can be used successfully to simulate the temperature environment on Lombok Island.

Leaf appearance rates are sensitive to temperature. In the environment on Lombok Island, leaf appearance rates were close to 0.2 leaves/day with an average phyllochron of 5 days. This rate is high, and the corresponding phyllochrons short, compared to those often reported at lower temperatures but they were comparable to the rates of leaf appearance and the phyllochron reported by Slafer and Rawson (1995b) for wheat grown at 25°C (0.18-0.19 leaves/day) but lower than the rate (0.24-0.33 leaves/day) reported by Rawson

(1993) for wheat grown at 30/25°C. Leaf appearance rates did not differ between Sembalun and Gunung Sari which had about a 5°C difference in growing season temperatures. This confirms earlier reports of the relative insensitivity of leaf appearance and final leaf number to temperature (Slafer and Rawson 1994b, 1995b). Therefore, rates of leaf appearance may not vary much between different locations on Lombok. When expressed in thermal time the phyllochrons measured (107-192°C.d) were longer than 100°C.d that is commonly quoted for wheat grown in the Australian cereal zone (Tennant et al. 2000) which reflects the supra-optimal temperatures under which the plants were grown.

The time to flower for all varieties other than Yitpi did not differ much between Gunung Sari and Sembalun despite a 5°C difference in mean temperature between them (Fig 3.2c). While crop development was occurring at temperatures above the optimum during the early stages, the optimum and base temperatures increase as the wheat plant develops (Slafer and Rawson 1995a) and it is likely that the period from stem elongation to anthesis was occurring at temperatures closer to the optimum. The similarity in flowering times at the two sites was consistent with previous studies that compared development at two temperatures similar to those measured at the two sites (Fig 3.2c). Nevertheless, the results suggested Yitpi may be more sensitive to high temperatures than the other varieties. The sensitiveness of Yitpi may related to the presence of winter vernalisation allele.

The study used a small set of eight genotypes to examine the influence of the PpD-1 and Vrn1 genes on wheat plant development on Lombok. Among these varieties, sensitivity to photoperiod was most important in determining flowering. Photoperiod sensitivity at *Ppd-D1* (*Ppd-D1a*) delayed flowering in the field experiments. The vernalisation genes were less influential and their influence differed between the two sites. They were more important at Gunung Sari where the winter alleles at Vrn-1A and Vrn-1B delayed double ridge (Vrn-1B) and flowering (Vrn-1A, Vrn-1B). In a more comprehensive study using a much larger data set, Eagles et al. (2010) demonstrated that photoperiod and vernalisation responsiveness interact to determine flowering time, but the effect of the photoperiod insensitive allele was greatest in genotypes with no or a single winter allele, which were typical of the genotypes used in the current study. Coincidentally, they found that the presence of the insensitive allele at Ppd-D1 advanced flowering by between 8 and 12 days, which is comparable to the effect measured on Lombok. These vernalisation and photoperiod genes accounted for less than half the genetic variation in heading date in the analysis of Eagles et al. (2010) who explained this by observing that flowering is also controlled by other developmental genes including other vernalisation and photoperiod genes (e.g. Kuchel et al. 2006, Bennet 2012) and earliness *per se* genes that are independent of vernalisation and photoperiod responsiveness (Snape et al. 2001). The influence of the earliness *per se* (Eps) genes on development in the field is not well understood. Although the effects of the *Eps* genes may be modulated by temperature, double ridge and flowering can be delayed considerably by a late allele (Lewis et al. 2008, Appendino and Slafer, 2003). The results from the present study presents *prima facie* evidence Eps trait may be important in this tropical environment because the effect of differences in BVP among varieties on flowering was greater than that accounted for by the photoperiod sensitivity allele at *PpD-1* locus. Midmore et al. (1982) suggested varieties possessing a vernalisation requirement may be useful in delaying the timing of TSI and extending the pre-flowering period, but the results from the field trials indicate the effects will be variable and may have a smaller influence than photoperiod sensitivity. Perhaps effects of high temperature and its long BVP may have accounted for large delay in flowering in Yitpi at Gunung Sari (Table 3.5, Fig 3.2c).

Variation in yield per plant among the 10 genotypes was related most strongly to grains per spikelet and the ears per plant and less so with kernel weight. Significant variation in early development occurred among the genotypes, but these were not strongly associated with yield. A similar conclusion was reached by Midmore et al. (1982) who also worked in tropical regions: they did not find an increase in grains per spikelet from a delay in early development and there was no relationship between the duration of the developmental phases and grain set. Variation in the development may have an indirect influence on yield potential by the timing of flowering in relation to environmental stresses rather than a direct effect of duration on spikelet and floret development.

In some environments, sowing time can have a major influence on yield potential. It was anticipated that in a tropical environment where daylength and temperature vary little through the year, time to flower would also show relatively small variation. This occurred at Sembalun but flowering was delayed at the earliest time of sowing at Gunung Sari and this response was most marked in Yitpi (Figure 3.2). This was surprising because there was only a small difference in temperature (<2°C) and daylength was slightly longer at the earliest sowing dates, which should have advanced flowering. Despite the significant correlations between mean temperature and time to flowering among the six sowing dates at Gunung Sari, the large response over such a narrow range in temperatures was surprising and suggests that some other environmental factor may be influencing the response. It is possible that the heavy rain and subsequent waterlogging at the three earliest sowing times at Gunung Sari, which delayed emergence and affected early growth, may have contributed to this response to sowing time. While this effect was exacerbated by above-average rainfall in 2010, rainfall during April and May can be high and waterlogging may occur in a number of years. This may reduce the reliability of early-sown crops.

5 CONCLUSION

Crop development was rapid but there was significant variation in the rates of development and time to flower among wheat varieties grown under continuously high temperatures. Based on the analysis of individual vernalisation and photoperiode genes, the major control of time to flower was photoperiod sensitivity with vernalisation requirement having a smaller and less consistent effect on development. However, there were differences in development that could not be completely explained by these effects and the influences of intrinsic earliness on develop in this environment warrants further study. Variation in the timing and duration of early stages of development appeared to have little effect on grain yield of wheat. Yield as more related to grain per spikelet and tillering,while tillering was affected by tiller production and tiller survival. Nevertheless, timing of flowering in relation to important environmental stresses, such as water logging, could have an important influence on yield in other seasons and requires further investigation on Lombok.

ACKNOWLEDGEMENTS

The first author thanks The Indonesian Department of Education, Directorate General of Higher Education (DIKTI) for providing financial support to undertake this study. We also thank Prof. Mansur Ma’shum and Dr. Dwi Ratna Anugrahwati of Mataram University Lombok-Indonesia for supporting field work in Lombok.

REFERENCES

Appendino, M.L., Slafer, G.A., 2003. Earliness per se and its dependence upon temperature in diploid wheat lines differing in the major gene Eps-A m1 alleles. Journal of Agricultural Science 141, 149-154.

Bagga, A.K., Rawson, H.M., 1977. Contrasting responses of morphologically similar wheat cultivars to temperatures appropriate to warm temperature climates with hot summers: a study in controlled environment. Australian Journal of Plant Physiology 4, 877-887.

Bonhomme, R., 2000. Bases and limits to using 'degree.days' units (Review). European Journal of Agronomy 13, 1-10.

Brougham, M., 2006. The relationship between vernalisation sensitivity, photoperiod sensitivity, basic vegetative period and grain yield in Australian wheat gerplasm. Honours thesis, University of Adelaide, Adelaide.

Eagles, H.A., Cane, K., Vallance, N., 2009. The flow of alleles of important photoperiod and vernalisation genes through Australian wheat. Crop & Pasture Science 60, 646-657.

Eagles, H.A., Cane, K., Kuchel, H., Hollamby, G.J., Vallance, N., Eastwood, R.F., Gororo, N.N., Martin, P.J. 2010. Photoperiod and vernalisation gene effects in southern Australian wheat. Crop & Pasture Science 61, 721-730.

FAO, 2013. FAO Statistics (http://www.fao.org/corp/statistics/en/). Food and Agriculture Organization of the United Nations, Rome Italy.

Fischer, R.A., 1985. Physiological limitations to producing wheat in semitropical and tropical environments and possible selection criteria. Wheats for more tropical environments. A proceedings of an international symposium on wheat production and research in tropical environments, held in Mexico on 24-28 September, 1984. CIMMYT, Mexico, pp. 209-230.

Gusmayanti, E., Pertiwi, S., Handoko, Risdiyanto, I., Machida, T., 2006. Determining potential wheat growing areas in Indonesia by using the spatial compromise programming technique. Agricultural Information Research 15, 373-379.

Handoko, I., 2007. Gandum 2000: Penelitian Pengembangan Gandum di Indonesia. SEAMEO BIOTROP, Jakarta.

Haun, J.R., 1973. Visual quantification of wheat development. Agronomy Journal 65, 116-119.

Ishag, H.M., Mohamed, B.A., 1996. Phasic development of spring wheat and stability of yield and its components in hot environments. Field Crops Research 46, 169-176.

Kuchel H, Hollamby G, Langridge P, Williams K, Jefferies SP, 2006.Identification of genetic loci associated with ear-emergence inbread wheat. Theoretical and Applied Genetics113, 1103–1112.

Kardono, Widiatminisih Winan, Agung Riyadi, Wahyu Purwanta (eds) (2012) Indonesia's technology needs assessment for climate change adaptations 2012. National Council on Climate Change of Indonesia Jakarta, Indonesia, 183pp.

Lewis S, Faricelli, ME, Appendino ML, Valarik M and Dubcovsky J, 2008. The chromosom region including Earliness *per se* locus Eps-A^m1 affects the duration of early developmental phases and spikelets number in diploid wheat. J. Exp. Bot. 59: 3595-3607

Medan-Bisnis, 2012. Kementan: Budaidaya gandum meluas dilakukan mulai 2014 (Dept. Agric.:Growing wheat commercially will be atarting in 2014). Medan Bisnis, Medan.

Midmore, D.J., Cartwright, P.M., Fischer, R.A., 1982. Wheat in tropical environments. I. Phasic development and spike size. Field Crops Research 5, 185-200.

Rahman, M.S., Wilson, J.H., 1978. Determination of spikelet number in wheat. III. Effect of varying temperature on ear development. Australian Journal of Agricultural Research 29, 459-467.

Rahman, M.S., Wilson, J.H., Aitken, Y., 1977. Determination of spikelet number in wheat. II. Effect of varying light level on ear development. Australian Journal of Agricultural Research 28, 575-581.

Rawson, H.M., Richards, R.A., Munns, R., 1988a. An examination of selection criteria for salt tolerance in wheat, barley and triticale genotypes. Australian Journal of Agricultural Research39: 759-72

Rawson, H.M., 1988b. Effects of high temperatures on the development and yield of wheat and practices to reduce deleterious effects. In: Klatt, A.R. (Ed.), Wheat production constraints in tropical environments. Proceedings of the international conference, Chiang Mai, Thailand, 19-23 January 1987., pp. 44-62.

Rawson, H.M., 1993. Radiation effects on rate of development in wheat grown under different photoperiods and high and low temperatures. Australian Journal of Plant Physiology 20, 719-727.

Rawson, H.M., Zajac, M., 1993. Effects of higher temperatures, photoperiod and seed vernalisation on development in two spring wheats. Australian Journal of Plant Physiology 20, 211-222.

Savin, R., Nicolas, M.E., 1996. Effects of short periods of drought and high temperature on grain growth and starch accumulation of two malting barley cultivars. Australian Journal of Plant Physiology 23, 201-210.

Shaykewich, C.F., 1995. An appraisal of cereal crop phenology modelling. Canadian Journal of Plant Science 75, 329-341.

Shpiler, L., Blum, A., 1986. Differential reaction of wheat cultivars to hot environments. Euphytica 35, 483-492.

Siregar, S., 2012. Impor Gandum Diperkirakan Capai 7,4 Juta Ton (Wheat import predicted to 7.4 Mt). Indonesia Finance Today. PT. Indonesia Finanindo Media, Jakarta.

Slafer, G.A., 1996. Differences in phasic development rate amongst wheat cultivars independent of responses to photoperiod and vernalization. A viewpoint of the intrinsic earliness hypothesis. Journal of Agricultural Science 126, 403-419.

Slafer, G.A., Rawson, H.M., 1994a. Sensitivity of wheat phasic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. Australian Journal of Plant Physiology 21, 393-426.

Slafer, G.A., Rawson, H.M., 1994b. Does temperature effect final number of primordia in wheat? Field Crops Research 39:111-117

Slafer, G.A. and Rawson, H.M 1995a. Base and optimum temepratures vary with genoptye and stage of development. Plant, Cell and Environment 18, 671-679.

Slafer, G.A. and Rawson, H.M. 1995b. Rates and cardinal temperatures for processes of development in wheat: effects of temperature and themal amplitude. Australian Journal of Plant Physiology 22, 913-926.

Snape, J.W., Butterworth, K., Whitechurch, E., Worland, A.J., 2001. Waiting for fine times: genetics of flowering time in wheat. Euphytica 119, 185-190.

Tennant, D., Siddique, K.H.M., Perry, M.W., 2000. Germination, vegetative and reproductive growth. In: Anderson, W.K., Garlinge, J.R. (Eds.), The wheat book; Principles and practise. Department of Agriculture, Western Australia, p. 321.

Warrington, I.J., Dunstone, R.L., Green, L.M., 1977. Temperature effects at three development stages on the yield of the wheat ear. Australian Journal of Agricultural Research 28, 11-27.

WMO, 2012. Weather Information for Lombok. World Meteorological Organisation (http://worldweather.wmo.int/043/c00654.htm).

Zadoks, J.C., Chang, T.T., Konzak, C.F., 1977. A decimal code for stages in the development of cereals. Weed Research 14, 415-421.

CHAPTER 4

ADAPTATION OF WHEAT TO A TROPICAL ENVIRONMENT

A Zubaidi[A], G Gill and GK McDonald[B]

School of Agriculture, Food and Wine

Waite Campus

University of Adelaide

PMB 1

Glen Osmond, South Australia, 5064

Australia

[A] University of Mataram

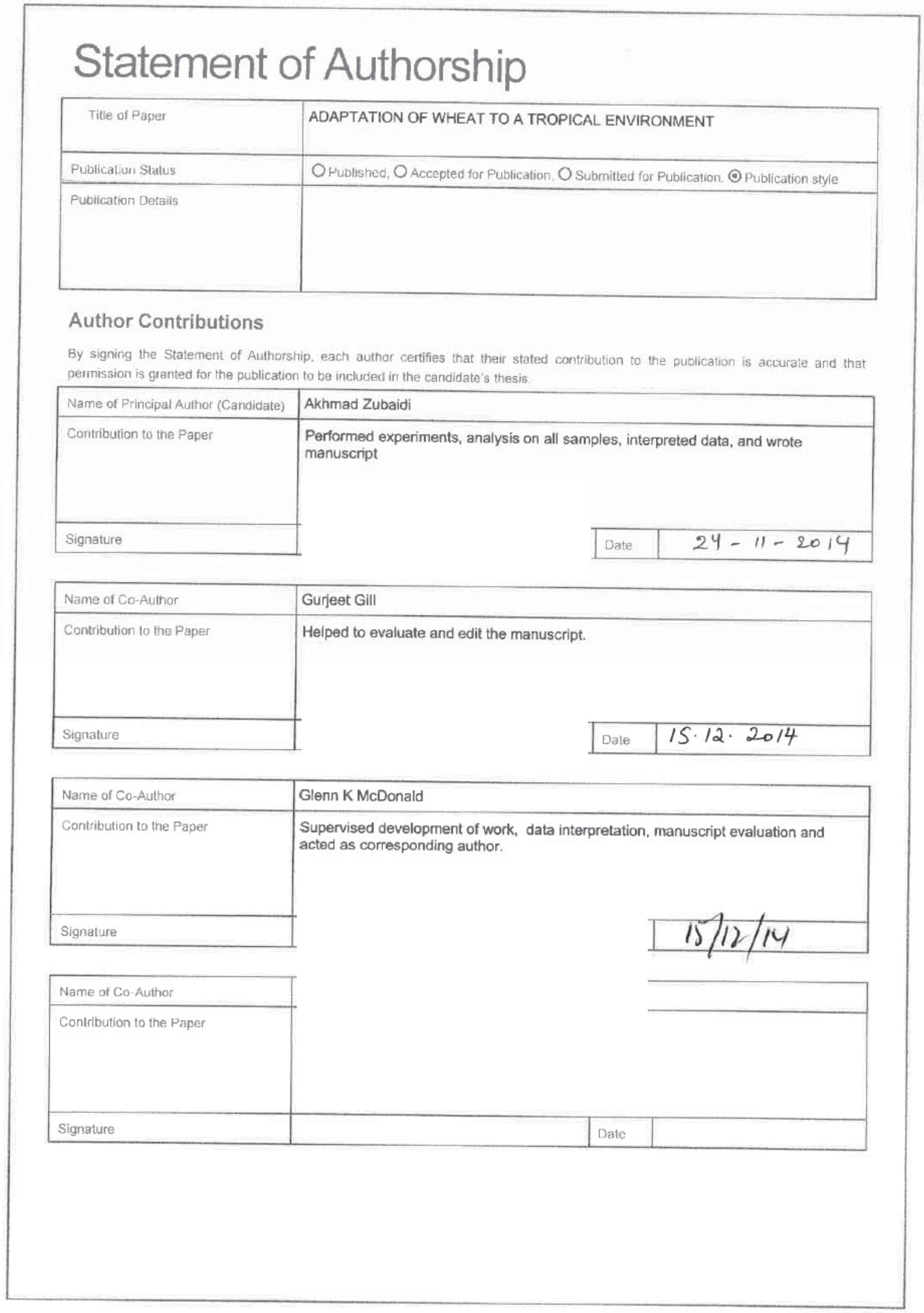
Lombok, Indonesia

[B] Corresponding author

Phone: +61 8 8313 7358

Fax: +61 8 8313 7109

Email: glenn.mcdonald@adelaide.edu.au



Statement of Authorship

Title of Paper	ADAPTATION OF WHEAT TO A TROPICAL ENVIRONMENT
Publication Status	○ Published, ○ Accepted for Publication, ○ Submitted for Publication, ● Publication style
Publication Details	

Author Contributions

By signing the Statement of Authorship, each author certifies that their stated contribution to the publication is accurate and that permission is granted for the publication to be included in the candidate's thesis.

Name of Principal Author (Candidate)	Akhmad Zubaidi		
Contribution to the Paper	Performed experiments, analysis on all samples, interpreted data, and wrote manuscript		
Signature		Date	24 - 11 - 2014

Name of Co-Author	Gurjeet Gill		
Contribution to the Paper	Helped to evaluate and edit the manuscript.		
Signature		Date	15 · 12 · 2014

Name of Co-Author	Glenn K McDonald		
Contribution to the Paper	Supervised development of work, data interpretation, manuscript evaluation and acted as corresponding author.		
Signature			15/12/14

Name of Co-Author			
Contribution to the Paper			
Signature		Date	

Abstract

Wheat is grown predominately in temperate areas around the work but there has been an expansion of production into subtropical and tropical areas. These environments are consistently warm, although temperatures are moderated by altitude and often with distinct wet and dry seasons. Wheat is not currently grown commercially in Indonesia, however Indonesia is a major importer of wheat, consumption of wheat is increasing and alternative dry season crops are required in parts of the country to help diversify farm income. One such area is Lombok Island, (8.5°S, 116.3°E) where the current cropping system consists of one or two rice crops during the wet season (September-April) followed by a dry season, non-rice crop (May-August). Two experiments were conducted in 2010 and 2011 to investigate the feasibility of wheat production on Lombok and the adaptation of wheat to the current cropping systems. Field experiments were carried out at 6 sowing times in 2010 and 3 sowing times in 2011 at 3 different sites, ranging up to 1000 m asl to represent low, medium and high elevation areas on the island. Eight Australian wheat varieties and 2 Indonesian varieties were selected to represent a range in maturity types.

Elevation had a large influence on productivity.Wheat reliably produced grain yields above 3 t/ha when grown at elevations above 500 m asl. The mean increase in yield with elevation was 250 kg ha^{-1} per 100m and this was associated with a decline in average growing season temperature from about 28°C to 17°C. The associated change in yield with temperature was -55 g $m^{-2}°C^{-1}$. At the lowland sites, yield increased as sowing was delayed from mid-April to early June, which corresponded to the period when temperatures and rainfall declined. At high elevation the optimum sowing time was mid-May to early June which also allowed flowering to occur in the cooler, drier part of the year. Early maturing varieties yielded relatively better at the lowland sites but at elevations above 500 masl, midseason varieties produced higher yields and their yields

were more responsive to seasonal growing conditions. Grain yield was strongly associated with grains m^{-2} in all environments.

Sowing wheat in May-early June at medium to high elevations of Lombok Island is an important part of a potential rice-wheat production system on Lombok. This allows the wheat crop to mature and be harvested in late August or early September before the onset of rainy season and the need for the next crop to be planted. This would allow wheat to fit in with the current cropping systems. The experiments also demonstrated the sensitivity of yield to growing season temperatures.

1. Introduction

Wheat (*Triticum aestivum* L) is one of world's major sources of dietary calories and protein. It is a temperate cereal that is grown over a wide range of precipitation and temperature conditions, mostly in the range from 25° to 50° latitudes. However, wheat production has expanded into tropical and subtropical areas, to less than 15°latitude due in part to the availability of more widely adapted semi-dwarf germplasm (Music and Porter, 1990; Badaruddin et al., 1999) as well as the growing demand for wheat-based products in these regions. In these tropical and subtropical environments, wheat is grown during the cool season and often at high altitude to minimise the adverse effects of high temperature

Currently, wheat is not produced in Indonesia, but it is the largest importer of wheat in South East Asia. This trend is likely to continue as the *per capita* consumption of wheat-based products continues to increase. The need to provide feed grain to support increased production of eggs, dairy and meat products is also likely to increase the demand for cereal grains. Increased production of wheat in Indonesia would help to ease the dependence on imported wheat for the country. However, improvement in the adaptation of wheat to tropical environments is needed to achieve this goal. Wheat is a winter cereal that evolved in temperate environments and tropical conditions are not favourable for wheat production. However, there is variation in rainfall and temperature during the year as well as topography that can be exploited to improve the growing environment for wheat.

Temperature and photoperiod are two environmental factors that greatly influence wheat development, growth and yield. Yield is affected by time of sowing and location because of the differences in temperature and photoperiod during the year and among different locations (Bauer et al., 1988). Changes in sowing date can alter the duration of some developmental stages significantly, and to different degrees depending on cultivars (Angus et al., 1981; Hay and Wilson, 1982; Kirby et al., 1985; Savin and Nicolas, 1996). However in tropical countries such as Indonesia, variation in photoperiod is small and it is likely that temperature will be a major factor influencing crop development and productivity.

Lombok Island in Indonesia (8.5°S, 116.3°E) has a hot and humid climate with distinct wet and dry seasons. The wet season stretches from October to April with 1295 mm of rainfall (average 215 mm per month) while the dry season lasts from May to September when only 219 mm is received (average 36 mm per month). Temperatures on Lombok are higher than those experienced in many other regions where wheat is grown. The average maximum temperature is 30.9ºC during the day and minimum temperature is 22ºC at night in the lowland areas, but temperatures are 5-10°C cooler in the upland areas in the centre of the island. The lowest maximum temperatures occur in July-August, while the lowest rainfall occurs during July-September (WMO, 2012) (Fig. 4.1).

The cropping system on Lombok consists of two rice and one non-rice crop, mainly peanut and soybean or sometimes maize. In drier areas, there is only one rice crop during the rainy season (October–January) followed by one non-rice crop and then a fallow until the next rainy season. An alternative crop to replace the fallow may help farmers diversify their cropping systems in these areas. Wheat is proposed as one of the non-rice options in the cropping system, which could be planted immediately after the second rice crop to use stored water in the soil for early growth and harvested before the start of rainy season in October. During this period, wheat will be growing at a time when temperatures are lowest and rainfall is declining (Fig.4.1).

Time of sowing and the maturity type of the variety will be important on Lombok to allow crop growth and development to match seasonal changes in temperature and rainfall and allow wheat to be integrated into the current agricultural systems. In many environments, sowing outside the ideal time can result in the loss of yield, which is related to reduction in germination or crop establishment (Baloch et al., 2010) and growth components such as dry matter accumulation and leaf area index (Dhaka et al., 2006). Time of sowing can also determine the length of the crop growth cycle and the timing of key stages of development in relation to the determination of the major yield components, grain number and thousand grain weight (Tahir et al., 2009). The importance of sowing time to wheat yield on Lombok is not known.

Elevation may influence wheat performance because of its influence on temperature, especially in the tropics, and may be important for the adaptation of wheat in tropical environments. Investigations on the influence of elevation on wheat growth and yield in tropical and subtropical areas have generally shown substantial increases in yield at higher altitudes in Rhodesia (Cackett and Wall, 1971), China (Li et al., 1983; Xiao et al., 2010), Venezuela (Vega and Vega, 1990) and Indonesia (Handoko, 2007). There is a large variation in elevation on Lombok and it is anticipated this will have a substantial influence on wheat yield.

The aim of this work was to examine the effects of sowing time and maturity type on the yield of wheat at sites with different elevations. Through these studies the feasibility of wheat production on Lombok and the integration of wheat into the current cropping systems would be better understood.

2. Materials and methods

Six field experiments were carried out in two growing seasons during 2010 and 2011 on Lombok Island, Indonesia (8.5°S, 116.3°E). Sites were chosen to represent low, medium and high elevation areas on the island.

2.1. Plant material

Plant material consisted of 8 Australian and 2 Indonesian bread wheat varieties. The varieties were selected to represent a range in maturity types (Chapter 3). The eight Australian varieties were used because of the lack of Indonesian varieties with a range in flowering times. The varieties grown were Axe, Silverstar (early flowering), Mira, Gladius, Hartog, Janz (midseason), Sunvale and Yitpi (late flowering). The two Indonesian varieties used were Nias and Dewata. These 10 varieties were grown in 2010, but in 2011 only Axe, Gladius, Nias and Dewata were grown as they showed the most promising results in 2010 and they represented a range in maturity types that was considered suited to Lombok (early and midseason).

2.2. Sites and weather

Three sites were chosen in each year to represent 3 different elevations. Experiments were conducted at Sembalun (1000m above sea level (m asl)), Narmada (200m asl) and Gunung Sari (10m asl) in 2010 and at Lekok (10m asl), Senaru (500m asl) and Sembalun in 2011. The sites at Gunung Sari, Narmada, Lekok and Senaru were rice fields where flooded rice was grown prior to the experiments. At Sembalun, fields are mainly used for growing vegetable crops, and mixed cropping of capsicum and strawberry occurred before the experiment in 2010 and cabbages were grown before the experiment in 2011. All sites were in farmer’s fields.

Soils were mixed silty to sandy loam at Narmada, and sandy loam at Gunung Sari and Sembalun. Composite soil samples were collected to a depth of 1m at each site to measure pH, electrical conductivity (EC), total soil organic carbon (C) and nitrogen (N), available phosphorus (P) and boron (B) (Table 4.1). The sites were acidic and non-saline with organic C concentrations ranging from 1-4% in the surface 10cm. Despite high applications of fertilizer, especially N, P and potassium (K) to the preceding rice crops, soil N and P were low at the lowland sites. In general, the site at Sembalun was more fertile than the lowland sites where rice was grown (Table 4.1).

Temperatures at the sites were monitored using Tiny Tag® data logger (Gemini Data Loggers), while rainfall data were obtained from nearby weather stations. The two experimental years represented contrasting seasons. In 2010, rainfall was 3-10 times greater than the long term average (Table 4.2). The heavy rainfall resulted in water-logging and poor germination and establishment at Gunung Sari and Narmada, and the first three sowing times were not harvested at Namada because of these adverse conditions. Monthly maximum temperatures consistently averaged about 31°C during the growing season at Gunung Sari while at Sembalun maximum temperatures averaged 28ºC. However the average minimum temperatures at Sembalun were 5-6ºC lower than at Gunung Sari. In 2011 rainfall was much less and close to the long-term average for the dry season. Growing season temperatures were lower as well, compared to 2010, and the differences between the sites were greater. Maximum temperatures at the high elevation site at Sembalun were 7-8°C (2011) lower than the coastal site (Lekok) while minimum temperatures were 8-9ºC lower (Table 4.2).

Table 4.1. Chemical properties of soils at the experimental sites on Lombok Island in 2010 and 2011

Sites	Depth (cm)	pH^A	EC^A (µS/cm)	Organic $Carbon^B$ (%)	Total N^C (%)	Available P^D (mg/kg)	$Boron^E$ (mg/kg)
				2010			
Gunung Sari	0-10	5.6	31.2	2.21	0.15	9.81	12.12
	10-20	5.7	21.1	0.72	0.06	7.88	26.12
	20-60	5.8	20.4	0.41	0.03	11.23	6.39
	60-100	5.8	25.7	0.60	0.04	13.44	51.87
Narmada	0-20	5.3	63.8	1.96	0.11	8.45	18.55
	20-60	5.8	24.8	0.79	0.06	5.94	24.47
	60-100	5.8	19.8	0.57	0.04	3.00	128.18
Sembalun	0-20	5.5	36.9	3.05	0.18	29.59	12.10
	20-40	5.6	24.7	2.03	0.12	20.17	14.62
	40-100	5.6	31.6	2.98	0.17	11.99	22.97
				2011			
Lekok	0-20	5.1	49.8	1.22	0.12	2.77	11.01
	20-40	5.3	61.0	0.96	0.09	1.75	11.53
	40-80	5.3	29.4	0.29	0.06	5.73	11.18
Senaru	0-20	4.6	96.0	1.14	0.11	2.34	10.31
	20-40	4.8	98.0	0.85	0.09	0.50	9.79
	40-80	4.6	53.0	0.62	0.06	1.34	13.06
Sembalun	0-20	5.1	89.9	4.12	0.17	8.72	16.50
	20-40	5.3	60.0	2.74	0.19	5.67	9.78
	40-60	5.3	65.9	3.13	0.20	0.94	11.32
	60-80	5.1	91.0	3.65	0.22	2.43	11.85

^{A} 1:5 soil: water extract; ^{B} Walkley-Black method; ^{C} Kjeldahl N; ^{D} Bray No 1 method; ^{E} Hot water extractable B

Table 4.2. Mean monthly minimum and maximum temperatures and rainfall at the six experimental sites in 2010 and 2011. Temperatures were measured by a data logger at each sites and rainfall was recorded at a nearby weather station

Year	2010									2011								
Site	Gunung Sari			Narmada[A]			Sembalun			Lekok			Senaru			Sembalun		
Month	Min. ºC	Max. ºC	R\fall (mm)	Min. ºC	Max. ºC	R\fall (mm)	Min. ºC	Max. ºC	R\fall (mm)	Min. ºC	Max. ºC	R\fall (mm)	Min. ºC	Max ºC	R\fall (mm)	Min. ºC	Max. ºC	R\fall (mm)
Apr	23.8	33.4	103			141	16.7	27.4	126			131			235			378
May	23.8	32.4	289			339	16.7	27.2	138	23.0	31.8	162	21.0	30.5	0	12.7	25.7	246
Jun	22.6	31.9	116			354	15.3	26.8	32	22.0	30.6	33	19.8	28.5	0	11.2	24.7	5
Jul	22.3	31.3	345			219	15.2	27.2	73	20.5	30.0	2	19.9	28.7	0	11.3	20.4	3
Aug	22.7	31.2	105			74	14.8	28.1	40	20.5	30.0	0	19.1	29.2	0	11.3	20.4	0
Sep	23.4	31.3	n/a				15.3	27.4		22.7	30.7	0	20.4	29.9	0			0

[A] temperature data were not available from Namada

2.3 Sowing dates

In 2010 each variety was sown 6 times at 2-weekly intervals between mid April and late June. This period encompasses the first half of the dry season when crops are sown (Fig 4.1). Sowing occurred within 1-2 days of each other at the three sites. Treatments consisted of a combination of 6 sowing dates and 10 varieties at each site. The sowing dates at Gunung Sari were 19 April, 3 May, 17 May, 31 May, 15 June, 28 June; at Narmada 17 April, 1 May, 15 May, 29 May, 12 June, 26 June; and at Sembalun 18 April, 2 May, 16 May, 30 May, 13 June and 27 June. In 2011, only three sowing dates were selected to represent early, mid-season and late sowing dates. Sowing dates were: Lekok, 20 May, 2 June, 20 June; Senaru, 21 May, 6 June, 18 June; and Sembalun 22 May, 7 June and 19 June.

2.3. Crop husbandry

Each field was cultivated after the previous crop to prepare the seed bed. At planting a basal compound fertilizer NPK (15-15-15) was applied at the rate of 300 kg/ha. Urea was applied at the rate of 135 kg N/ha and was split into 3 times of application: planting, 21 DAS and 35 DAS. Youngest unfolded leaves from 5-6 plants from the second sowing time were sampled at 6 weeks after sowing for tissue analysis by Inductively Coupled Plasma (ICP) spectroscopy (Wheal et al., 2011). Leaf tissue analysis in general showed adequate amounts of P, K and sulphur (S), however the tissue analyses indicated boron (B) was deficient at Gunung Sari and marginally deficient at other sites (1.9-2.9 mg kg^{-1}). Deficiency of manganese (Mn) was also detected at Sembalun (8-12 mg kg^{-1}). Therefore, in 2011 B and Mn were also applied as a foliar spray.

In 2010, the amount of seed available and the need to run experiments in farmers' fields limited the size of the plots, which were 3 rows wide and 1 m long with 30cm row spacing. Sixty seeds were sown for each variety at Sembalun and 80 seeds at the 2 other sites

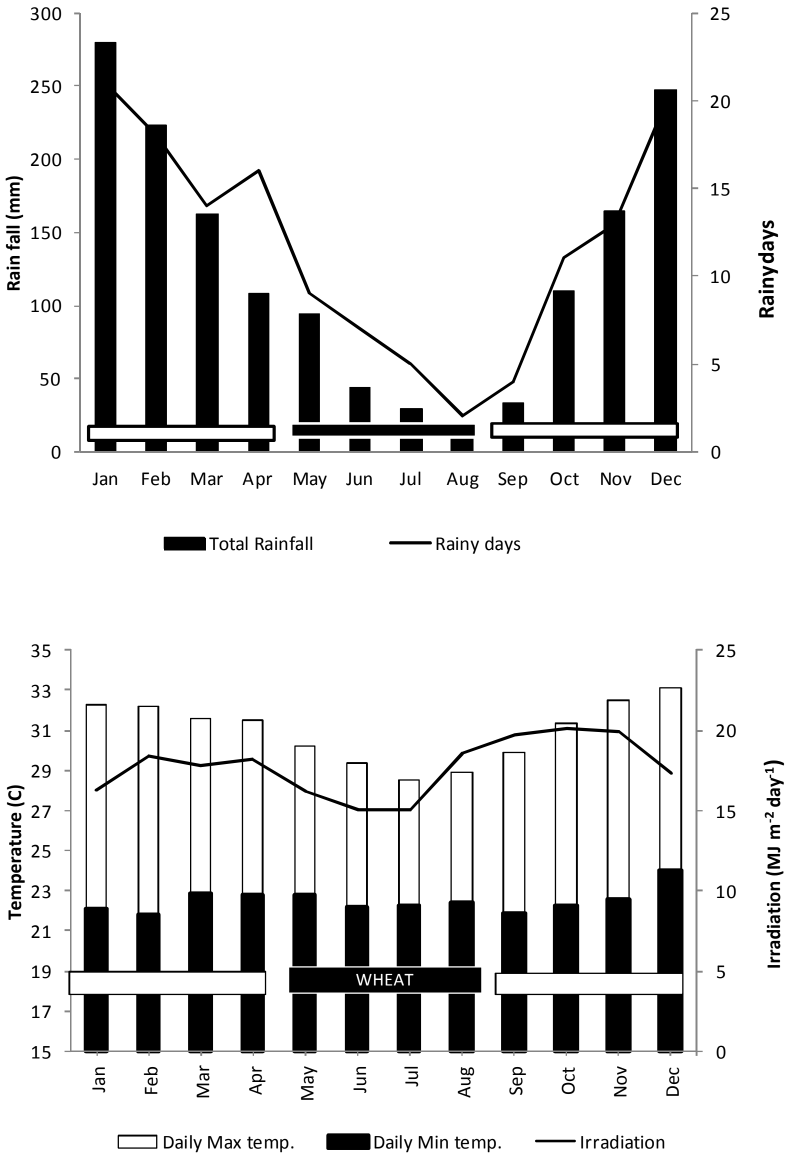


Fig 4.1. Long term average of daily maximum and minimum temperature and total rainfall and rainy days for Lombok Island (WMO, 2012) (http://worldweather.wmo.int/043/c00654.htm), and Irradiation of nearby area Denpasar (8°45’S-115°10’E) (Morrison and Sudjito, 1992). Closed bars indicate growing season in which wheat is proposed, during the coolest month May to August and the open bars represent the current rice growing seasons.

due to likelihood of lower establishment following a rice crop. After 2 weeks, plants were thinned to 40 plants per row (133 plants m^{-2}) at Sembalun, while at the 2 other sites only 25 plants per row (83 plants m^{-2}) were recovered due to the germination and establishment problems caused by high rainfall at these sites. Increased availability of seed allowed the plot size to be bigger in 2011. Seeds were sown in 1.5m x 5m plots, in 5 rows with 30 cm spacing. Three hundred seeds were sown in each row and thinned to 200 seedlings per row (133 plants m^{-2}) two weeks after sowing. Hand weeding was done as needed, 2–3 times at all sites except at Senaru, where a pre-sowing herbicide was applied a week before planting.

2.4. Experimental designs

An objective of the 2010 experiment was to span a wide range of sowing times at the three sites to characterise the responses to sowing time. However, because of the limited supplies of seed and the small areas available in the farmers' fields, the varieties were grown in non-replicated plots at each sowing time and multiple plant samples were taken from each plot to provide an estimate of variation associated with each treatment. Each sowing time was sown in a block with varieties randomly allocated within a block. In 2011, with fewer sowing times and larger quantities of seed, the experiments were designed as randomised complete blocks, with 3 replicates.

2.5. Measurements of plant growth and development

In 2010, data were collected on individual plants in each plot. Ten plants were chosen randomly from the middle row of each plot and tagged. Crop development stage (Zadoks et al., 1977) and tiller number were measured on the tagged samples during the growing season at each sowing date. Time to flowering, when 50% of ears had reached anthesis (Zadoks growth stage 65), was recorded. At maturity 10 plant samples from each plot were harvested from the central section of the middle row and taken to the laboratory at the Mataram University. Plants were cut at ground level, put into harvest bag and dried in an oven at 60ºC for 2 days. Subsequent measurements of yield and yield components were made on each individual plant. Total dry matter was weighed for biomass production. Spikelet number and total grain number were counted and grains/head was estimated from all the heads produced by each plant sampled. Plant biomass and grain yield per plant were multiplied by the plant population to estimate productivity on an area basis.

In 2011, measurements of tillering, growth stages and dry matter were made during the season. Half of each plot was used for destructive dry matter measurements, while the other half was used for maturity harvest and yield estimations. Tiller numbers were recorded weekly or fortnightly. Dry matter production was measured by harvesting plant samples at stem elongation (Zadoks growth stage (ZGS) 31), flag leaf emergence (ZGS 39), anthesis (ZGS 65) and maturity.

Plants were sampled from a 0.5m length in two adjacent rows. The plants were cut at ground level, put into plastic bag and taken to the Agronomy Laboratory University of Mataram for measurements. Samples were put into oven at 60ºC for 2 days then weighed. Tillers and head number were also recorded.

At maturity quadrat samples were taken to estimate yield components, (ear number/plant, spikelets number/ear and grain/spikelet, harvest index (HI) and 1000 grain weight) and from the remaining half of each plot all the ears were harvested, sun dried and threshed to recover grains, and grains were weighed to estimate grain yield.

2.6. Data analysis

The lack of replicated plots in 2010 means that varieties and sowing dates were used as pseudo-replicates to estimate the main effects of sowing date and variety. For each site, variety was used as replication to test the average effect of sowing date, while sowing date was used as replication to test the effect of varieties. As an aim of the analysis was to examine the importance of maturity more so than individual varieties, varieties were classified as early (Axe, Nias, Silverstar,), midseason (Dewata, Gladius, Hartog, Janz, Mira)and late (Sunvale, Yitpi) and maturity grouping was used as a fixed effect in the analysis of variance. In 2011 the use of replicated treatments allowed the interactions between sowing time and variety to be examined. Data were analysed as a multisite trial to examine the interactions between site, variety and sowing date. Data from 2011 were also analysed using pseudoreplicates like the 2010 data, as a check of the method of analysing data in 2010. The analysis showed similar treatment effects using pseudoreplicates and using replicated treatments (Suplementary Table 4.1).

All data were analysed with GenStat statistical program. Differences between mean values were compared by 5% least significant differences (LSD) and relationships between variables were examined using simple linear correlations and regression.

3. Results

3.1. Plant development

Plant development in general was rapid but there were differences among the different maturity groups and locations (Chapter 3). Table 4.3 shows the average times to stem elongation, flowering and maturity for the four varieties that were common to both years. In 2010 time to the start of stem elongation (GS31) was 7-10 days later at Sembalun compared to Gunung Sari. The early varieties (Axe and Nias) reached GS31 5-7 days before the midseason varieties (Gladius and Dewata). Crops flowered, on average, between 40 and 60 days after sowing with the two earlier varieties flowering 7-10 days before the midseason

Table 4.3.Times to the beginning of stem elongation (ZGS 31, Zadoks et al. 1977), flowering (ZGS 65) and maturity of 4 varieties of bread wheat on Lombok Island. Data are the averages± sem over all sowing times at each site.

		Days to:		
Site	Variety	GS31	50% flowering	Maturity
		2010 (n = 6)		
Gunung Sari	Axe	28.6 ± 1.3	44.2 ± 3.4	78.2 ± 2.8
	Gladius	35.6 ± 2.8	59.8 ± 2.8	97.2 ± 7.7
	Nias	33.0 ± 2.5	51.8 ± 3.6	88.8 ± 7.6
	Dewata	39.4 ± 3.8	66.2 ± 3.4	102.0 ± 5.0
Sembalun	Axe	32.0 ± 1.0	49.8 ± 1.2	94.3 ± 2.2
	Gladius	39.3 ± 1.7	59.3 ± 0.9	109.5 ± 2.1
	Nias	34.3 ± 2.2	51.3 ± 2.2	97.5 ± 1.0
	Dewata	41.8 ± 1.6	66.0 ± 2.0	109.5 ± 2.1
		2011(n = 3)		
Lekok	Axe	21.1 ± 2.1	39.7 ± 2.2	76.7 ± 5.8
	Gladius	30.3 ± 1.5	51.3 ± 1.5	98.0 ± 2.5
	Nias	27.3 ± 1.8	43.0 ± 0.6	87.7 ± 2.3
	Dewata	33.3 ± 1.7	54.3 ± 1.9	98.3 ± 2.7
Senaru	Axe	25.3± 2.7	41.3 ± 1.2	91.3 ± 4.3
	Gladius	31.7 ± 4.4	53.7 ± 1.5	105.0 ± 0.6
	Nias	28.0 ± 4.0	45.0 ± 1.2	93.3± 2.8
	Dewata	32.7 ± 4.7	55.0 ± 0.6	105.0 ± 0.6
Sembalun	Axe	32.7 ± 1.3	57.7 ± 1.7	108.7 ± 1.9
	Gladius	40.0 ± 2.0	68.3 ± 0.9	120.7 ± 2.7
	Nias	34.3 ± 2.3	62.7 ± 1.2	112.7 ± 4.6
	Dewata	39.7 ± 2.3	70.3 ± 1.5	120.7 ± 2.7

varieties. There was relatively little difference between the sites in the time to flower. Crops at Sembalun reached maturity 7-10 days later than at Gunung Sari.

In 2011, time to GS31 was similar at the lowland sites (Gunung Sari and Lekok) and at Sembalun and at both sites the time was comparable to those recorded in 2010. Time to flowering was also similar to 2010 at the lowland sites (Gunung Sari and Lekok), but it was 10-20 days later at Sembalun. The mid-altitude site at Senaru was similar to Lekok for the time to GS31 and flowering, but was intermediate between Lekok and Sembalun for the time to maturity. As in 2010, the two early maturing varieties reached GS31 5-7 days earlier than the midseason varieties and reached flowering about 10 days earlier.

Difference in maturity among the sites were greater in 2011, with crops grown at Sembalun reaching maturity up to 30 days later than at Lekok. The post anthesis period (flowering to harvest ripe) ranged from 30-40 days in 2010 and 30-50 days in 2011 (Table 3).

In 2010, sowing at the earliest dates at Gunung Sari delayed flowering, which could be associated with other environmental factors than temperature such as waterlogging that delayed emergence, reduced crop establishment and slowed early growth, while at Sembalun no effect of time of sowing on flowering time was observed (Chapter 3).

3.2. 2010 experiment

3.2.1. Grain yield and yield components

Average grain yields in 2010 were 48 g m^{-2} at Gunung Sari, 78 g m^{-2}at Narmada and 323g m^{-2}at Sembalun (Table 4.4). High yields at Sembalun were achieved because dry matter production, ear production, grain set, thousand grain weight and HI were higher than at Gunung Sari and Narmada (Table4. 4). Maturity type influenced yield at the three sites. At Gunung Sari, average yields were highest among the early maturing varieties, while at Narmada and Sembalun midseason varieties produced the highest yields (Table 4.4). Late flowering varieties produced low yields at all sites. The effect of maturity on yield reflected differences in pre-anthesis growth (ear number, spikelets ear^{-1}) and consequently the number of grains m^{-2}, more than post-anthesis growth. The late maturity varieties produced smaller grains than the early and midseason varieties at all sites.

Table 4.4.Average yield, total dry matter at maturity and yield components of varieties grown at three sites in Experiment 1 in 2010, grouped according to maturity type. Data are the means across six sowing times.

Maturity type[A]	Yield (g m^{-2})	DM (g m^{-2})	Ears m^{-2}	Grain m^{-2}	Spikelet ear^{-1}	Grains spikelet^{-1}	TGW (g)	HI (%)
				Gunung Sari				
Site mean	48	265	307	2251	10.8	0.6	21.5	17.3
Early	66 a	256	310 b	2762 a	10.4 b	0.8 a	25.0 a	22.7 a
Midseason	45 b	280	318 b	2204 b	11.6 a	0.6 b	21.2 b	16.1 b
Late	33 c	252	401 a	1850 b	9.4 c	0.5 c	17.4 c	13.3 c
LSD.	8	ns	26.5	387	0.25	0.09	1.33	2.09
				Narmada				
Site mean	78	284	313	3819	10.5	1.3	28.5	20.5
Early	68 b	208 c	225 a	2956 c	10.4 b	1.4 a	22.7 a	31.5 a
Midseason	94 a	337 a	313 b	4547 a	11.6 a	1.3 a	20.9 b	29.1 b
Late	51 c	314 b	425 a	3384 b	9.7 c	0.9 b	14.9 c	17.2 c
LSD.	4	21.4	19.4	358	0.48	0.11	0.99	2.33
				Sembalun				
Site mean	323	848	507	11280	12.2	2.0	38.5	28.6
Early	293 b	760 b	477 b	10471 b	11.5 b	2.0 a	28.2 b	39.2 a
Midseason	344 a	888 a	482 b	11567 a	13.0 a	2.0 a	29.6 a	39.0 a
Late	307 b	875 a	614 a	11754 a	11.2 b	1.9 b	26.4 c	35.7 b
LSD.	0.27	70.0	32.5	852	0.32	0.04	0.6	1.52

[A] Early: Axe, Silverstar, Nias; Midseason: Mira, Gladius, Hartog, Janz, Dewata; Late: Sunvale, Yitpi.

Average responses to sowing time varied among sites (Fig. 4.2; Supplementary Table 3.1). At Gunung Sari grain yields increased with later sowing dates, while at Sembalun there was an optimum sowing data of 10 May after which yields declined. There were too few sowing dates at Narmada to indicate a general pattern in the response to time of sowing, but among the three sowing dates harvested, there was no effect of time of sowing on yield.

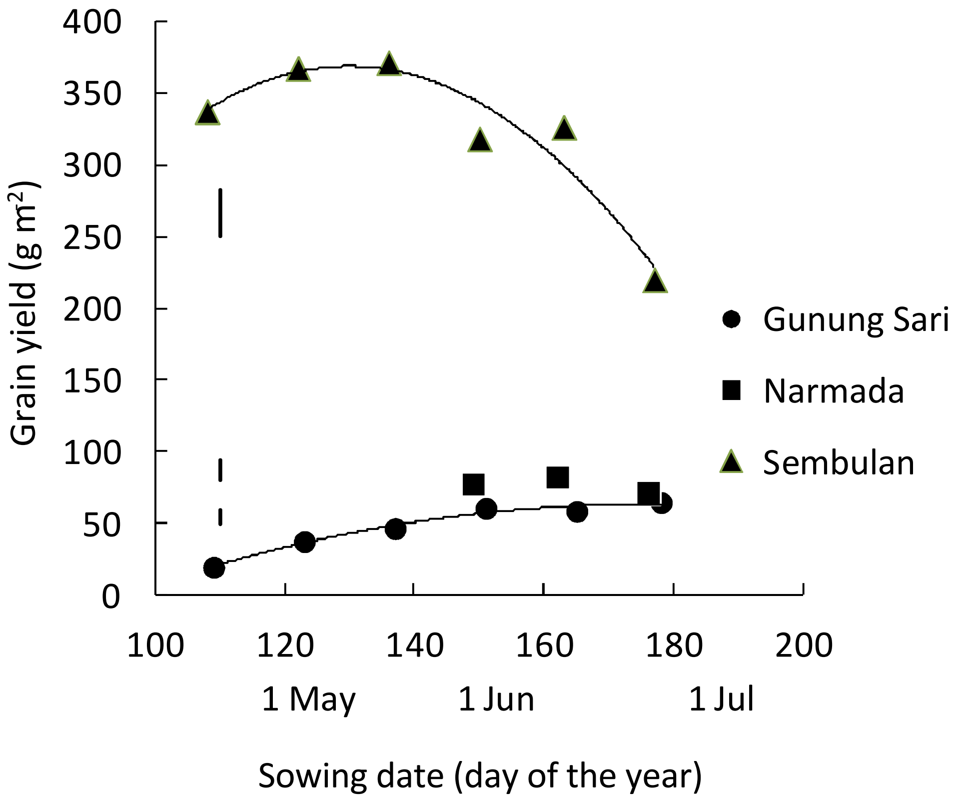


Fig 4.2. The average responses to sowing time of wheat sown at three sites on Lombok Island, Indonesia in 2010. The LSD (*P*= 0.05) for comparisons among sowing dates at each site are shown as vertical bars. The predicted optimum sowing date for Sembalun is 10 May (day 130). Grain yield from three sowing dates was only available at Namada because of water logging at the first three sowing times

Yields at these three sowing times at Narmada were similar to those measured at lowland site at Gunung Sari. Different yield responses were seen with flowering time: at Gunung Sari low yields occurred at early sowing and higher yields later,, while at Sembalun yield decreased with later anthesis date, with an optimum flowering time of 8 July (Fig. 4.3). Among both sites and sowing dates, grain yield was more strongly related to grains m^{-2} than to thousand grain weight (Fig. 4.4).

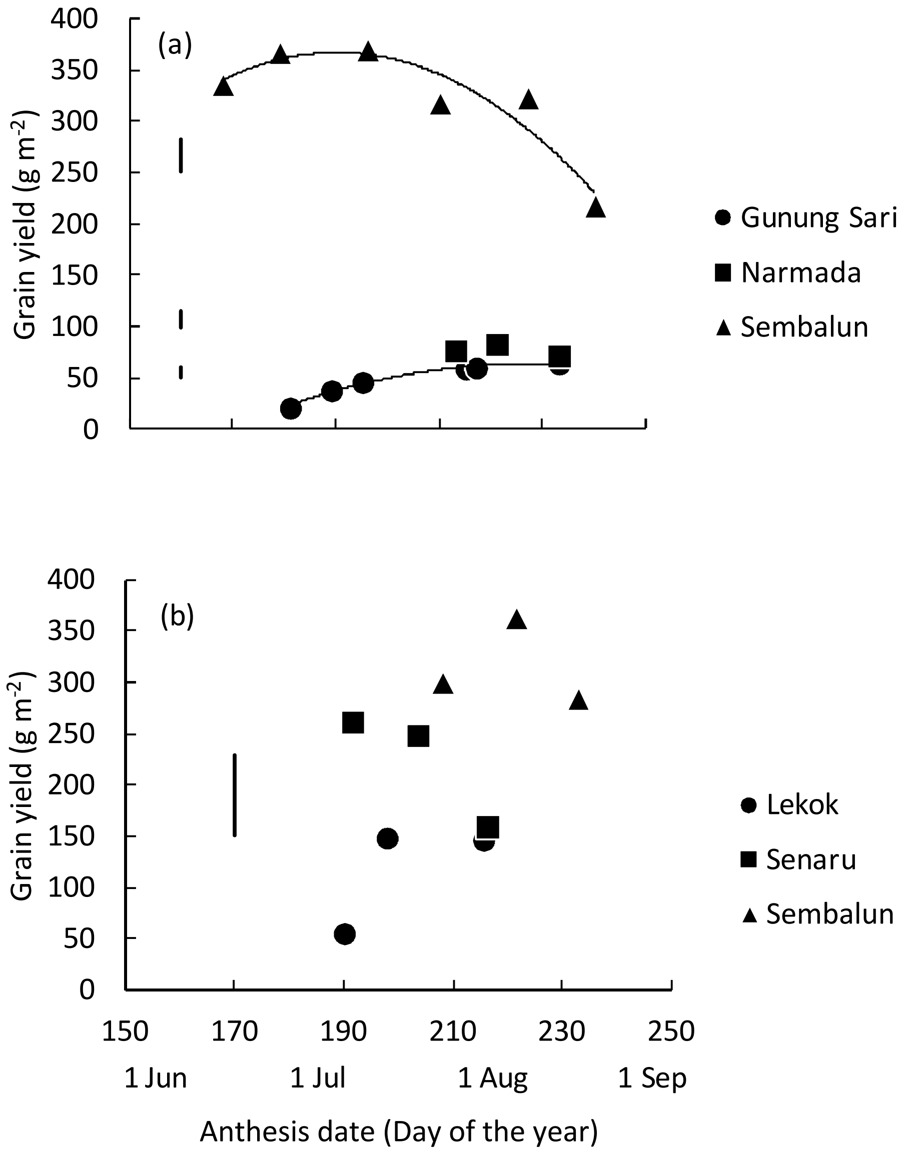


Fig 4.3.The average effect of time of flowering on the yield of wheat at three locations on Lombok Island in (a) 2010 and (b) 2011. The LSD (*P* = 0.05) for comparisons among sowing dates for each site in 2010 and for the Site x Sowing date interaction in 2011 are shown. The predicted optimum sowing date for Sembalun in 2010 is 8 July (day 190). Grain yield from three sowing dates was only available at Namada in 2010 because of water logging at the first three sowing times.

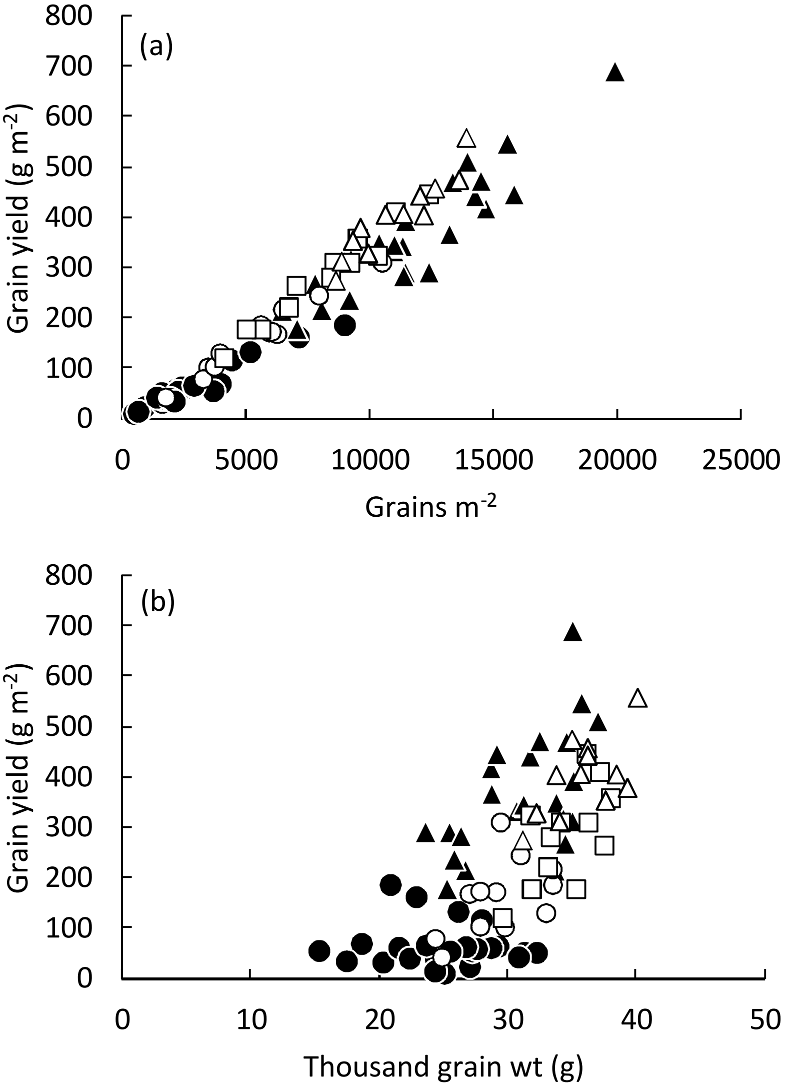


Fig 4.4. The relationships between grain yield and (a) grains m^{-2} and (b) thousand grain weight for the varieties Axe, Gladius, Nias and Dewata sown in 2010 (closed symbols) and 2011 (open symbols). The sites are Gunung Sari (●), Lekok (○), Senaru (□) and Sembalun (▲, Δ). Narmada was excluded because of lack of data

The two Indonesian varieties, Nias and Dewata, were high yielding at each site. At Gunung Sari, the early flowering Indonesian variety Nias produced the highest yield of all 10 varieties (110 g m^{-2}) while at Sembalun, Dewata and Nias were the two highest yielding varieties (494 g m^{-2} and 359 g m^{-2} respectively). At Narmada they produced average yields (Nias: 81 g m^{-2} and Dewata: 90 g m^{-2}). Of the Australian varieties Gladius produced the highest yield at Narmada (126 g m^{-2}) and produced a similar yield to Nias at Sembalun. (349 g.m^{-2}). The variation in yields among varieties was largely associated with the production of grains m^{-2}.

The above average rainfall in 2010 resulted in a high incidence of diseases. Wheat ears showed symptoms of Fusarium head blight (FHB) during grain filling that influenced seed production and the quality of grains. In some heads all seeds were affected. The incidence of FHB was more severe on Australian varieties compared to the tall Indonesian varieties, and the severity of FHB was greater at Gunung Sari and Narmada than at Sembalun.

3.3. 2011 Experiment

3.3.1. Plant growth

The Australian midseason variety Gladius tillered most while the Indonesian varieties Dewata and Nias showed similar patterns of tillering. All these varieties lost 20-30% of their tillers before maturity (Fig 4.5a). Axe developed very rapidly in this environment and did not produce large numbers of tillers and all those produced formed ears. Tillering was highest with a June sowing (Fig 4.5c) and at Sembalun (Fig 4.5e). The rapid development and short growing season at Lekok resulted in few non-fertile tillers being produced.

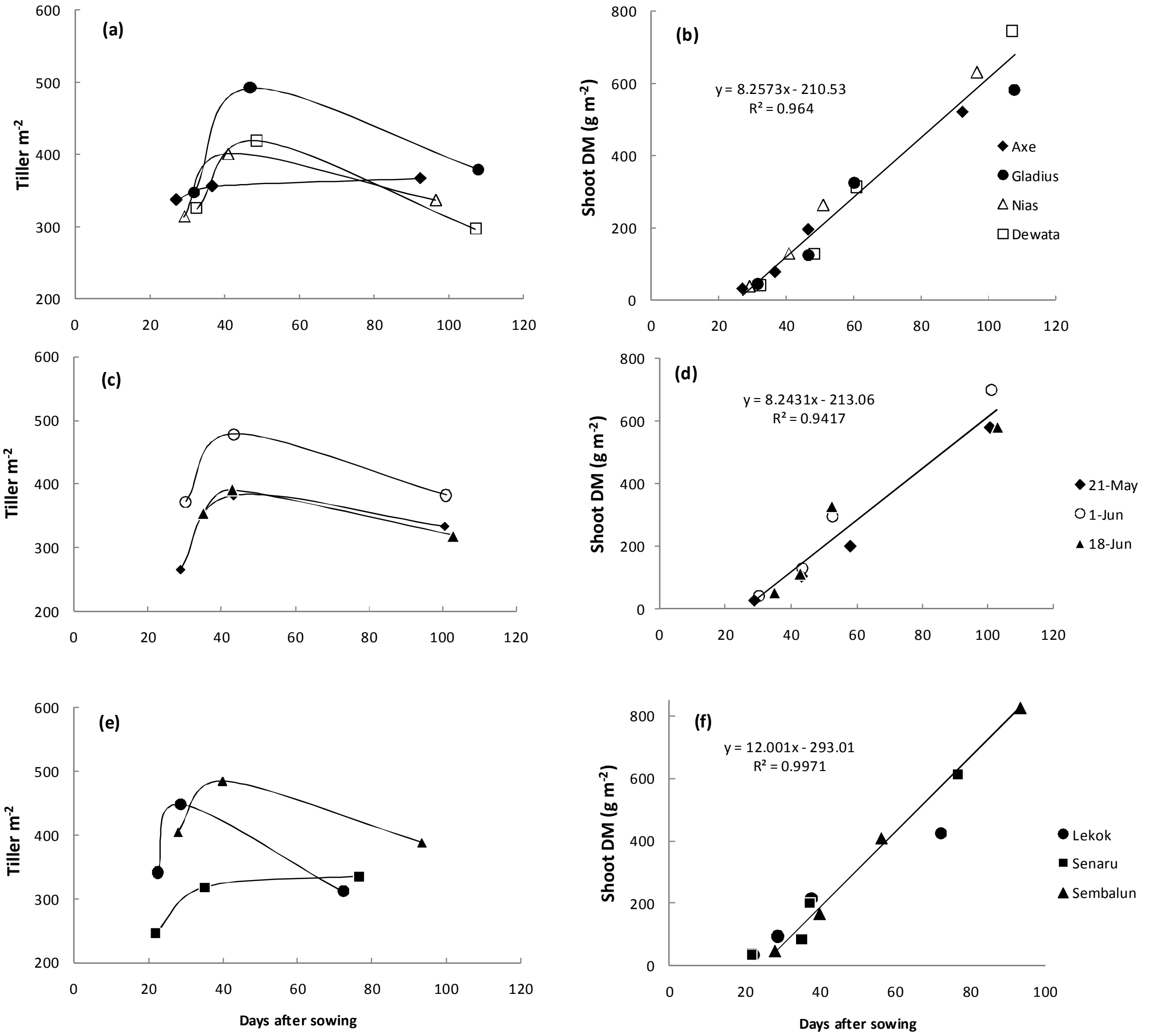


Fig 4.5. Change in tiller number (a, c, e) and shoot dry matter (b, d, f) of plants in 2011 based on days after sowing for different varieties (a, b), sowing dates (c, d) and sites (e, f).

Therefore, the rates of dry matter production were the same among the 4 varieties (Fig 4.5b), sowing times (Fig 4.5d) and sites (Fig 4.5f) and so differences in dry matter accumulation were associated with differences in the duration of growth. Average growth rates across sites were 12 g/m^2/d. The maximum dry matter accumulation of Axe was the

lowest of all varieties because it developed most quickly and matured early. Similarly, plants at Lekok produced the lowest dry weight because of the shorter growth duration.
Plant dry matter increased linearly with time over the period of measurement and statistical analysis found no significant difference in the regressions describing crop growth.

3.3.2. Yield and yield components

Grain yields were highest at Sembalun followed by Senaru and least at Lekok (Table 4.5; Supplementary Table 2). Crops at Sembalun produced the highest dry matter, grains m^{-2} and kernel weights (Supplementary Table 2).

There was no significant interaction between sowing time and variety at any of the sites. However, the response to sowing time differed significantly among the three sites with two different responses to sowing date (Table 4.5). At Lekok lowest yields were obtained from the first time of sowing with no significant difference between the two later sowings in June. In contrast, at Senaru and Sembalun, grain yields at the first two sowing dates did not differ significantly from one another, with the third sowing date producing the lowest yield. The responses in yield to sowing time reflected the responses in total dry matter and grains m^{-2} and consequently yield was strongly associated with grain number (Fig 4.4). Thousand grain weights increased with later sowing and were highest at Sembalun and lowest at Lekok. As in the first experiment, the yield response to anthesis date mirrored the response to sowing date (Fig. 4.3b).

3.4. Crop development and yield

The influence of different phases of growth on grain yield, grains m^{-2} and thousand grain weights was examined using simple linear correlations. The data for the lowland sites (Gunung Sari and Lekok) were examined separately from the upland sites (Sembalun and Senaru) because of the marked difference in yield; however in both cases yield was strongly

Table 4.5.The responses to sowing date among varieties of bread wheat sown at three sites on Lombok Island in 2011.Grain yield is based on bulk harvest of half the plot while grain number and thousand grain weight as derived from quadrat samples

	Site			Mean
Sowing date	Lekok	Senaru	Sembalun	
	Grain yield (g m^{-2})			
20 - 22 May[A]	56	262	301	206
2 - 7 June	149	249	364	254
18 - 20 June	147	160	285	198
Mean	117	224	317	
LSD	Site 45; Sowing time 45 Site x Sowing time 79			
	Total dry weight (g m^{-2})			
20 - 22 May	221	664	844	576
2 - 7 June	493	761	824	693
18 - 20 June	559	415	787	587
Mean	424	613	818	
LSD	Site 108; Sowing time 108 Site x Sowing time 186			
	Grains m^{-2}			
20 - 22 May	3048	8473	11610	7710
2 - 7 June	6567	9826	11880	9424
18 - 20 June	6601	6149	9731	7494
Mean	5406	8149	11073	
LSD	Site 1316; Sowing time 1316 Site x Sowing time 2279			
	Thousand grain wt (g)			
20 - 22 May	26.7	33.8	35.2	31.9
2 - 7 June	31.2	35.0	35.2	33.8
18 - 20 June	29.8	34.5	36.7	33.7
Mean	29.2	34.4	35.7	
LSD	Site 1.61; Sowing time 1.61 Site x Sowing time NS			

[A] Range of sowing times among the three sites

Table 4.6.Correlation between grain yields with grains m^{-2}, thousand grain weight, time to stem elongation (GS31), anthesis (GS65), maturity (GS90), durations of stem elongation to anthesis and anthesis to maturity at lowland and upland sites.

	Grain yield	Time to			Duration	
		GS31	GS65	GS90	GS31-GS65	GS65-GS90
Lowland sites (n = 31; mean yield = 98 g m^{-2})						
Grain yield		-0.202	-0.442*	0.085	-0.546**	0.489**
Grains m^{-2}	0.957***	-0.172	-0.397*	0.007	-0.503**	0.356*
Thousand grain wt	0.435*	-0.178	-0.326	0.219	-0.362*	0.551**
Upland sites (n = 37; mean grain yield = 353 g m^{-2})						
Grain yield		0.324*	0.496**	0.455**	0.371*	0.076
Grains m^{-2}	0.952***	0.274	0.372*	0.351*	0.246	0.079
Thousand grain wt	0.434*	0.201	0.463**	0.391*	0.452**	-0.007

correlated with grains m^{-2} and only weakly with thousand grain weight (Table 4.6). At the two lowland sites, late flowering and a long period between the start of stem elongation and flowering were associated with low grain number and yields. However a long post-flowering period was associated with high thousand grain weight and yield. In contrast, at the upland sites, the duration of the post-flowering period was not associated with yield, but instead high yields were associated with late flowering and a long pre-flowering period.

3.5. Effect of elevation

Grain yield was influenced by elevation, which was associated with variation in growing season temperature. Regression analysis suggested that average grain yield increased by 25g m^{-2} per 100 m increase in elevation (Fig. 4.6a). The data also suggested an optimum average

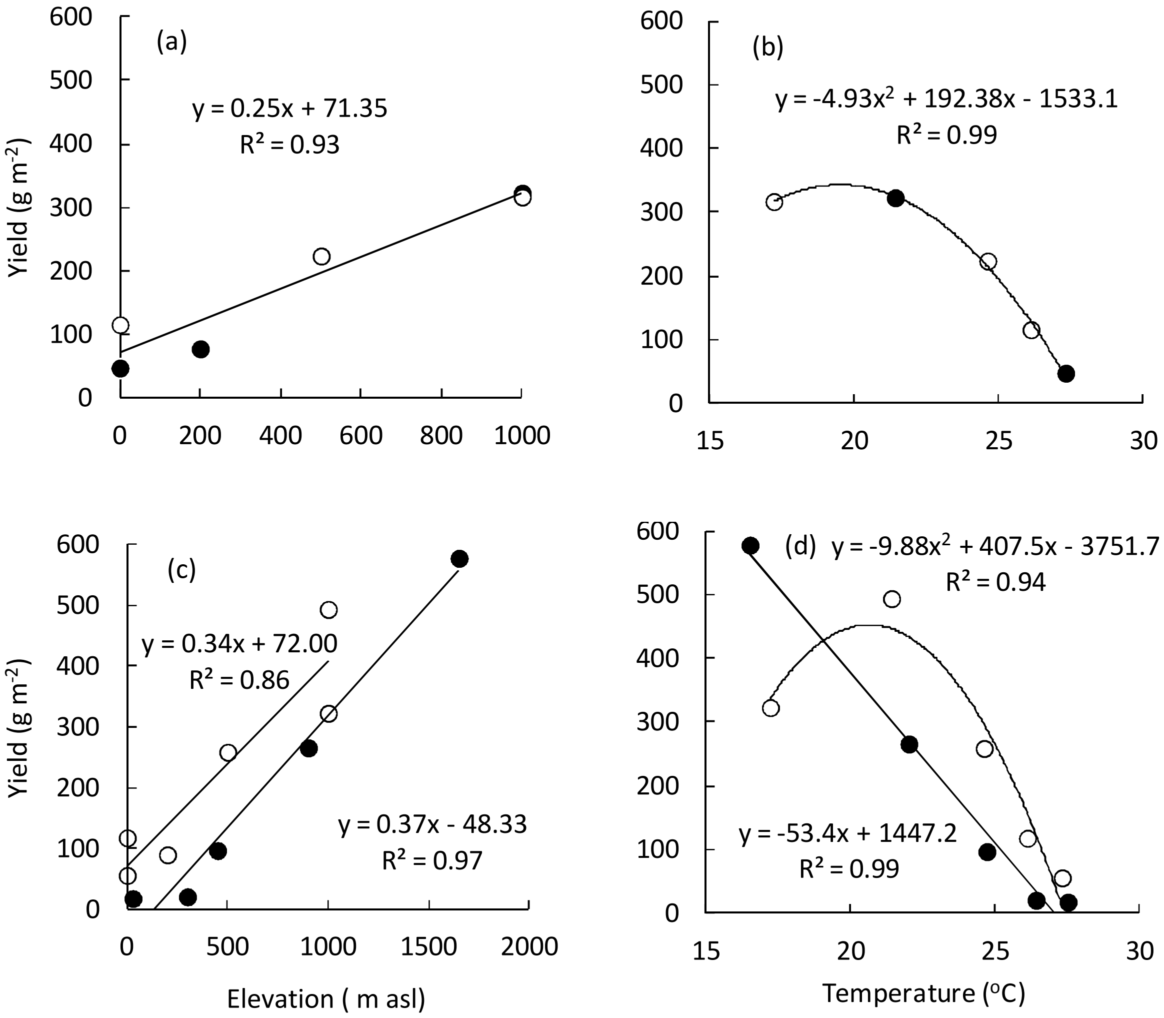


Fig 4.6. The relationships between elevation and growing season mean temperature on the grain yield of bread wheat on Lombok Island, Indonesia. The relationships in 2010 (●) and 2011 (○) is between site mean yield and (a) altitude and (b) temperature. The results of Handoko (2007) on Java Island (●) are compared with the results from Lombok Island (○) for the variety Dewata between yield and (c) elevation and (d) growing season temperature.

daily temperature for the growing season of 19.5ºC (Fig. 4.6b). The effect of elevation on the yield of the Indonesian variety Dewata is consistent with the previous analysis of Handoko (2007) on Java Island, with an average yield increase of 34 g m^{-2} per 100m increase in elevation, which was not significantly different to the 37 g m^{-2} per 100m derived from the work of Handoko (2007) (Fig. 4.6c). However the temperature response data for Dewata did not show an optimum on Java, while the results from Lombok suggest an optimum temperature of 21ºC (Fig. 4.6d).

4. Discussion

Introduction of wheat production into tropical environments such as Lombok Island needs to consider the environmental limitations and the prevailing farming systems in the area. Soil and weather, including temperature and rainfall, are among the environmental factors that could have a large influence on wheat growth and development. The trends in grain yields on Lombok were similar to widely published research which shows higher yield at sites with greater elevation (Cackett and Wall, 1971; Li et al., 1983; Vega and Vega, 1990; Handoko, 2007; Xiao et al., 2010). In Handoko's trials on Java Island, Indonesia (6-8°S; 106-112°E), Dewata (originally DWR 162) achieved a yield of 5.7 t/ha at high elevation (1650 m asl) (Handoko 2007). At elevations of 1000m or lower on Lombok Island (8°S; 116°E), yields were about 100g m^{-2}higher compared to those reported by Handoko (2007) but the effect of changes in elevation on yield was very similar (Fig. 4.6). The difference in yield may be associated with difference in solar radiation, because there is a significant transition from west to east in solar radiation in the Indonesian archipelago (Morrison and Sudjito, 1992). There is higher solar radiation and a higher proportion of clear days in the eastern islands compared to

Java, which may promote growth and yield in the eastern islands such as Lombok. Nevertheless, the yield data shows that wheat could be a viable crop on Lombok, especially at medium to high elevations of around 500masl and above.

Like many low-latitude environments, the potential growing season for wheat on Lombok Island is short and characterising the response to sowing date and elevation is important to develop the most appropriate management practices. There were significant effects of sowing time on grain yield where, depending on the location, early or late sowing resulted in lower yields. Consequently, the optimum sowing time varied with location, and this was reflected in the relationship between yield and flowering date. Despite this clear effect of sowing time on yield, the reasons for these yield trends are not easily explained because of the small monthly variation in temperature and solar radiation. This can be due to factors like waterlogging and disease. At lowland sites such as Gunung Sari the occurance of heavy rainfall at the three early sowing times causing waterlogging, while at higher site Sembalun, late sowing exposed plants to rain at the start of the wet season which increased the incidence of FHB.

In a general sense, the highest yields were achieved when flowering occurred during the cooler and drier months of the year. At the low elevation sites on Lombok (Gunung Sari and Lekok) for example, highest yields were achieved with sowing between the end of May and the end of June, which corresponded to crops flowering during the first two weeks of August in 2010 (Fig 4.3a) or the last two weeks of July in 2011. This period corresponds to the driest part of the year when temperatures are slightly lower and when average solar radiation increases (Fig. 4.1). At the medium-high elevation (Senaru) and high elevation (Sembalun) sites where temperatures are lower, crop development is slower (Table 4.3) and the highest yields were obtained with crops sown in mid-May to early June, with lower yields from later sowings (Figs. 4.2 and 4.3). These sowing times also resulted in flowering between early July and early August (Fig. 4.3).

Although yield improved with late sowing at the lowland sites, sowing late into June will cause the crops to flower in August and fill grain during September, which coincides with the start rainy season (Fig. 4.1). Late sown crops would be exposed to rain and high humidity at flowering and during grain filling, which will increase the risk of infection diseases such as FHB. The low yields produced at early planting at the lowland sites could be due to several reasons. There were greater problems with establishment at early sowings in 2010 because of the heavy rainfall and this may be exacerbated by growing wheat after rice. The acceleration of plant growth and developmental phases under early sowing also reduced the number of tillers, spikelets/head, and kernels/spikelet (Supplementary Table 1), and consequently reduced plant yield. Shorter duration of floral initiation and spikelet development associated with high temperatures may also limit the number of spikelets and florets formed. After August, maximum temperatures increase rapidly above 30°C, and flowering at such temperatures may also cause sterility(Saini and Aspinall, 1982). The narrow flowering window at the lowland sites and the pervasive high temperatures which limits growth and yield suggest that reliable wheat production in these environments may not be feasible.

The difference in yield at low elevation sites between 2010 and 2011 was mainly due to the differences in rainfall. Rainfall in 2010 was very high in Indonesia, including Lombok Island, where it was 3-10 times higher than the long term average,resulting in very wet soils and waterlogging at low elevation sites at Gunung Sari and Namada. The detrimental effects of these wet conditions would have been made worse by the higher temperatures experienced in 2010. At the high elevation site at Sembalun,which received less rainfall than Gunung Sari and where waterlogging was not a problem, variation in yield between 2010 and 2011 was less. The main effect of the high rainfall in 2010 at Sembalun was the development of dark staining on the grain and the development of leaf disease.

The late flowering varieties in 2010 consistently produced the lowest yields at all sites which was associated with poor grain set and grain growth. This may have been associated

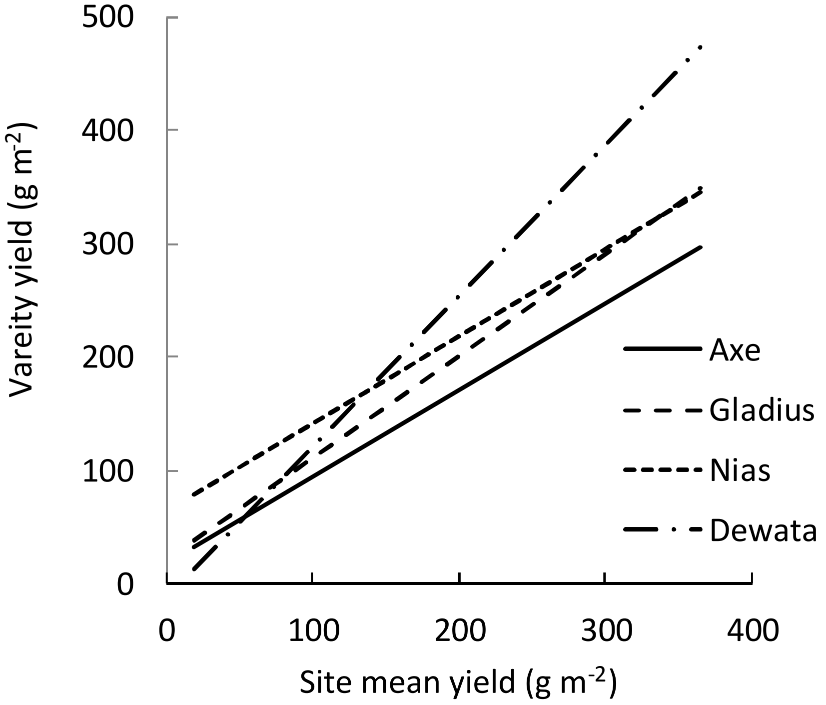


Fig 4.7. The regressions of variety yield against site mean yield derived from trials conducted in 2010 and 2011 for the Australian wheat varieties Axe and Gladius and the Indonesian varieties Nias and Dewata. The equations of the lines (n=24) are:

Axe: $Y = 18.497 + 0.762X$ ($r^2 = 0.659$)

Gladius: $Y = 21.459 + 0.892$ ($r^2 = 0.832$)

Nias: $Y = 62.966 + 0.776X$ ($r^2 = 0.651$)

Dewata: $Y = -14.044 + 1.338X$ ($r^2 = 0.755$)

with the greater exposure to higher temperatures at flowering and during grain filling. Early and midseason varieties showed differences in their adaption to different sites on Lombok, (Fig 4.7) and the two Indonesian varieties were generally higher yielding than the two Australian varieties (Fig 4.7). The Indonesian midseason variety Dewata in particular was highly responsive to improved growing conditions. This analysis is consistent with the apparent difference in the importance of pre-flowering and post-flowering growth at the

lowland and upland sites (Table4.6). The negative influence of late flowering and a long stem elongation phase on grain yield suggests that early flowering varieties perform relatively better in these lowland environments, while at the upland sites the later flowering midseason varieties produced higher yields. This difference in the adaptation between the early and midseason varieties may influence the types of varieties developed in the future. The early maturing varieties, Axe and Nias, performed relatively better at the low yielding, lowland sites, although Nias was consistently 45 g m^{-2} higher yielding across all environments. Axe is a very early maturing variety (Table 4.3) and under the warm growing conditions of Lombok, it develops rapidly and may produce insufficient biomass to develop a high yield potential. The midseason varieties showed a greater responsiveness to higher yielding conditions. The results suggest that if the medium to high elevation sites are to be the target for future wheat production, midseason varieties should be developed.

The Indonesian varieties, Nias and Dewata, were better adapted to the Lombok environment in both years. They were capable of producing high number of grains m^{-2}which was associated with their high spikeletshead^{-1} and they can form a foundation for future genetic improvement. These two lines were originally developed from Indian lines and they have traits that are suited to tropical environments. The higher yield of Nias and Dewata were not only because of high temperature resistance but could aslo due to better disease resistance or better waterlogging tolerance. More detailed studies of the characteristics of these lines is warranted as they may be useful sources of tolerance to some of the abiotic and biotic stress that occur on Lombok.

Lombok's current farming system consists of two rice crops grown during the rainy season and a non-rice crop or fallow during the dry season. The planting of the first rice crop starts in September/October when the rainy season begins, followed by a second rice planting season in January/February. The third planting, which occurs during the dry season, starts in May/June, at the end of the rainy season or at the beginning of the dry season. Wheat is suitable as a choice after the second rice crop, both at medium and high elevation where the timing of the start of the dry season matches with the best sowing time for wheat. However, the response to sowing time at low elevations such as Gunung Sari and Lekok suggests wheat will not easily fit into the cropping sequence as a third crop at all sites. There are three benefits of using wheat as the third crop on Lombok: (a) wheat will not replace rice which is much preferred by Lombok farmers (Gusmayanti et al., 2006), (b) it fits in with the current cropping sequence since the best sowing time coincides with the beginning of the dry season and it allows it to be grown during the coolest part of the year, and (c) maturity coincides with the dry season avoiding high occurrence of pest and diseases, and avoiding risk of sprouting of grain before harvest. Wheat production on Lombok is feasible at elevations above about 500 m but it is unlikely to be sustainable at lowland sites because of low yields and high incidence of disease. The growing season for wheat in the proposed rice wheat system on Lombok will coincide with the time when ambient temperatures and rainfall are the lowest (Fig. 4.1). The results of this study show that crops sown at the start of the dry season (May-June) reached flowering during the coolest period (July-August) of the year (Fig. 4.3). This proposed sowing time gives the greatest possibility of achieving high wheat yields on Lombok.

The effect of elevation on yield was generally consistent with previous studies in Indonesia by Handoko (2007) and the main driver of the response was temperature, which influenced the rates of development and the severity of heat stress. However the level of solar radiation in different parts of the Indonesian archipelago may also influence yield. The mean temperatures experienced during the growing season on Lombok are generally higher than those experienced in many other wheat growing areas. Eventhough growth of wheat during all development phases can be influenced by temperature (Slafer et al., 1994), the period leading up to flowering is still the most sensitive to heat because it coincides with an important yield forming period (Fischer, 1975). Although the range in temperatures on Lombok is small, the cooler conditions around flowering appear to have an important influence on yield. The importance of the pre-anthesis phase to the yield of wheat on Lombok was shown by the strong relationship between grain m^{-2} and yield, which was consistent across both years and sites. As well, the yield responses to sowing time were mirrored in the responses to anthesis date, which emphasised the importance of flowering time to yield on Lombok. Consequently, managing the crop to minimise the impact of heat stress at this time may be an important aspect of growing wheat on Lombok. The data across the different experiments suggested an optimum temperature for growth on Lombok of about 20°C.

Apart from time of sowing and variety, plant nutrition may have an important role in the productivity of crops on Lombok and will be an important component of the development of wheat production systems. Observations during the experiments showed the soils on Lombok to be low in organic matter, N, P and micronutrients, especially B and Mn, and this could be one of constraints of wheat growth in Lombok. Both B and Mn deficiencies were diagnosed in crops. Boron deficiency causing sterility has been reported to be a major limitation to wheat productivity in many tropical regions (Rerkasem et al., 1993; Dell and Huang, 1997; Rerkasem and Jamjod, 2004) and it cannot be ruled out as a factor contributing to the low grain set measured in some of the trials. Manganese deficiency can cause low yields by reducing yield components such as ear length, thousand grain weight and grains/ear

(Xu et al., 2010), inhibit absorption of nitrogen (Salem et al., 2004; Tai et al., 2004), inhibit synthesis of amino acid and protein (Tai et al., 2004) and yield loss (Kirchmann and Eskilsson, 2010). Application of micronutrients especially B and Mn together with macronutrients, N, P, may help overcome the problem. Liming could also help to increase soil pH and available phosphorus.However further work on the nutrition of wheat will be required to develop reliable recommendations.

5. Conclusion

Wheat reliably produced grain yields above 3 t/ha when it was grown at elevation around 500 m asl and above. In these areas the wheat production cycle can fit into the current cropping systems in these areas. Sowing wheat at the optimum time (May-early June) on the medium to high elevation of Lombok Island could be an important part of the wheat production system on Lombok. Sowing between May to early June is important to allow crop maturity and harvest in late August or early September before the onset of rain season and ensure timely planting of the next crop. At lowland sites, grain yields are be much lower and it is likely that crop maturity and harvest would overlap with the rainy period which will reduce grain quality as well as delay the planting of the next paddy rice crop.

Acknowledgement:

We thank Indonesian Department of Education, Directorate General of Higher Education (DIKTI) for the scholarship to do this work.

References:

Angus, J.F., Mackenzie, D.H., Morton, R., Schafer, C.A., 1981. Phasic development in field crops. II. Thermal and photoperiodic responses of spring wheat. Field Crops Research 4, 269-283.

Badaruddin, M., Reynolds, M.P., Ageeb, O.A.A., 1999. Wheat management in warm environments: effect of organic and inorganic fertilizers, irrigation frequency, and mulching. Agronomy Journal 91, 975-983.

Baloch, M.S., Shah, I.T.H., Nadim, M.A., Khan, M.I., Khakwani, A.A., 2010. Effect of seeding density and planting time on growth and yield attributes of wheat. JAPS, Journal of Animal and Plant Sciences 20, 239-242.

Bauer, A., Garcia, R., Kanemasu, E.T., Blad, B.L., Hatfield, J.L., Major, D.J., Reginato, R.J., Hubbard, K.G., 1988. Effect of latitude on phenology of "Colt" winter wheat. Agricultural and Forest Meteorology 44, 131-140.

Cackett, K.E., Wall, P.C., 1971. The effect of altitude and season length on the growth and yield of wheat (Triticum aestivum L.) in Rhodesia. Rhodesian Journal of Agricultural Research 9, 107-120.

Dell, B., Huang, L., 1997. Physiological response of plants to low boron. Plant and Soil 193, 103-120.

Dhaka, A.K., Bangarwa, A.S., Pannu, R.K., Malik, R.K., Garg, R., 2006. Effect of sowing time and irrigation on growth and yield of different wheat genotypes. Agric. Sci. Digest 26, 249-252.

Fischer, R.A., 1975. Yield potential in dwarf spring wheat and the effect of shading. Crop Science 15, 607-613.

Gusmayanti, E., Pertiwi, S., Handoko, Risdiyanto, I., Machida, T., 2006. Determining potential wheat growing areas in Indonesia by using the spatial compromise programming technique. Agricultural Information Research 15, 373-379.

Handoko, I., 2007. Gandum 2000: Penelitian pengenbangan gandum di Indonesia (Wheat 2000: Wheat research and development in Indonesia). SEAMEO_BIOTROP, Jakarta.

Hay, R.K.M., Wilson, G.T., 1982. Leaf appearance and extension in field-grown winter wheat plants: the importance of soil temperature during vegetative growth. Journal of Agricultural Science, UK 99, 403-410.

Kirby, E.J.M., Appleyard, M., Fellowes, G., 1985. Variation in development of wheat and barley in response to sowing date and variety. Journal of Agricultural Science, UK 104, 383-396.

Kirchmann, H., Eskilsson, J., 2010. Low manganese (Mn) and copper (Cu) concentrations in cereals explained yield losses after lime application to soil. Acta Agricultura Scandinavica. Section B, Plant Soil Science 60, 569-572.

Li, C., Zhang, H., Lin, D., 1983. Response of winter wheat Triticum sativum cultivar Fengmai-13 to the climate at different altitudes. 2. Accumulation and partitioning of dry matter of aerial part. Acta Botanica Yunnanica 5, 301-304.

Morrison, G.L., Sudjito, 1992. Solar radiation data for Indonesia. Solar Energy 49, 65-76.

Music, Porter, 1990. Wheat. In: Stewart, B.A., Nielson, D.R. (Eds.), Irrigation of Agricultural Crops. ASA - CSA - CSSA, Madison - Wisconsin.

Rerkasem, B., Jamjod, S., 2004. Boron deficiency in wheat: a review. Field Crops Research 89, 173-186.

Rerkasem, B., Netsangtip, R., Lordkaew, S., Cheng, C., 1993. Grain set failure in boron deficient wheat. In: Barrow, N.J. (Ed.), Plant nutrition - from genetic engineering to field practice: Proceedings of the Twelfth International Plant Nutrition Colloquium, 21-26 September 1993, Perth, Western Australia., pp. 401-404.

Saini, H.S., Aspinall, D., 1982. Sterility in wheat (Triticum aestivum L.) induced by water deficit or high temperature: possible mediation by abscisic acid. Australian Journal of Plant Physiology 9, 529-537.

Salem, H.M., Nadia, M.B., Farid, I.M., 2004. Growth enhancement of wheat by supplementation of N, Fe, Mn, and Zn. Annals of Agricultural Science, Moshtohor 42, 2101-2113.

Savin, R., Nicolas, M.E., 1996. Effects of short periods of drought and high temperature on grain growth and starch accumulation of two malting barley cultivars. Australian Journal of Plant Physiology 23, 201-210.

Slafer, G.A., Connor, D.J., Halloran, G.M., 1994. Rate of leaf appearance and final number of leaves in wheat: effects of duration and rate of change of photoperiod. Annals of Botany 74, 427-436.

Tahir, I.S.A., Nakata, N., Yamaguchi, T., Nakano, J., Ali, A.M., 2009. Physiological response of three wheat cultivars to high shoot and root temperatures during early growth stages. Plant Production Science 12, 409-419.

Tai, C., Wu, T., Wang, J., 2004. Studies of Mn deficiency on the physiological effects of wheat genotypes. Acta Agriculturae Boreali-Sinica 19, 53-56.

Vega, O.U.A., Vega, J.A., 1990. Response of wheat and triticale varieties to different altitudes in Venezuela. Revista de la Facultad de Agronomia, Universidad Central de Venezuela 16, 13-26.

Wheal, M.S., Fowles, T.O., Palmer, L.T., 2011. A cost-effective acid digestion method using closed polypropylene tubes for inductively coupled plasma optical emission spectrometry (ICP-OES) analysis of plant essential elements. Analytical Methods 3, 2854-2863.

WMO, 2012. Weather Information for Lombok (http://worldweather.wmn.int/043/c00654.htm). World Meteorological Organisation.

Xiao, G., Zhang, Q., Li, Y., Wang, R., Yao, Y., Zhao, H., Bai, H., 2010. Impact of temperature increase on the yield of winter wheat at low and high altitudes in semiarid northwestern China. Agricultural Water Management 97, 1360-1364.

Xu, F., Wang, X., Xie, J., Ding, D., Chen, L., 2010. Nutrition effect of Mn in manganese tailings on wheat growth. Guizhou Agricultural Sciences, 56-58, 61.

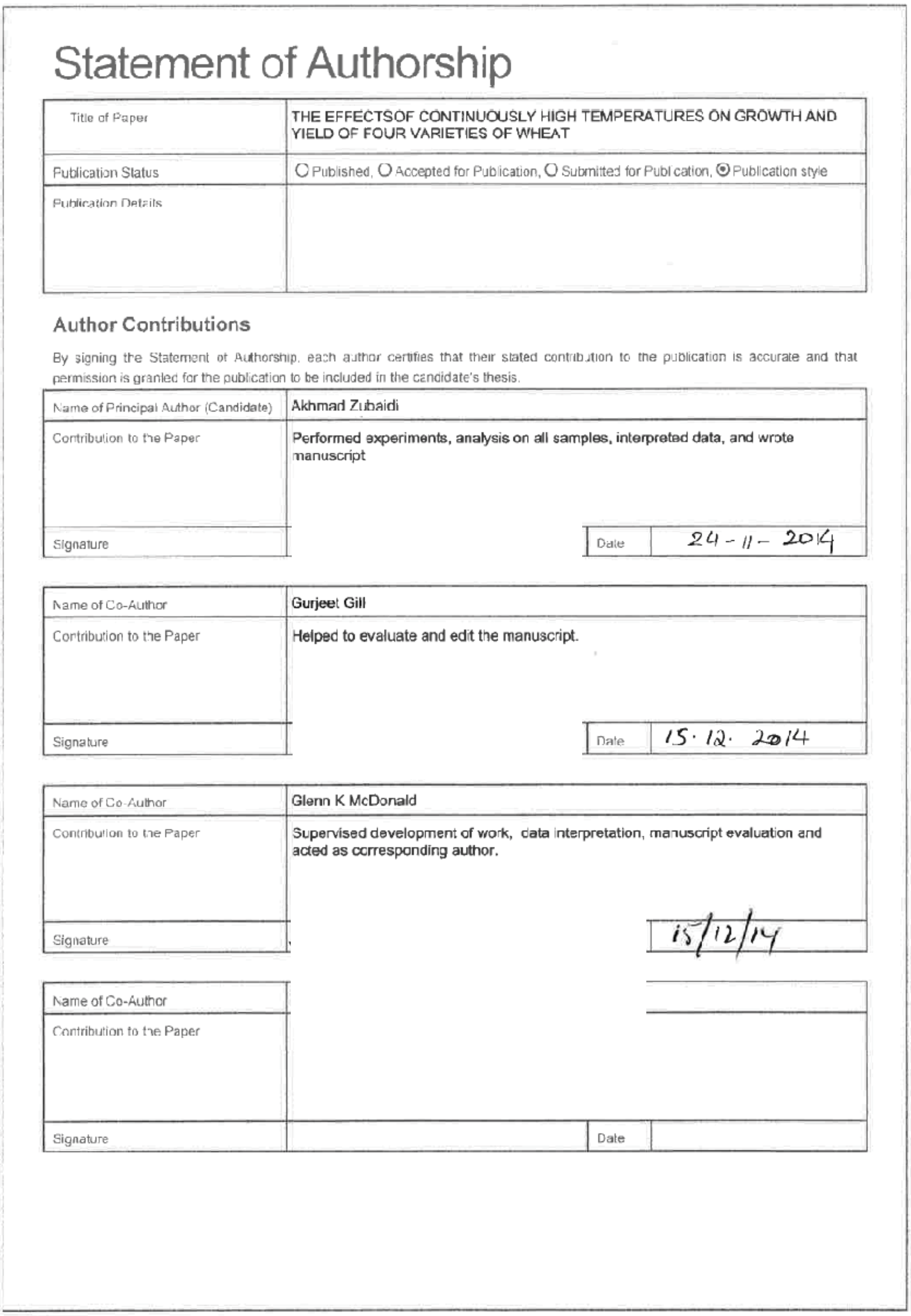
Zadoks, J.C., Chang, T.T., Konzak, C.F., 1977. A decimal code for stages in the development of cereals (Un code decimal pour les stades de croissance des cereales). Phytiatrie-Phytopharmacie 26, 129-140.

CHAPTER 5

THE EFFECTSOF CONTINUOUSLY HIGH TEMPERATURES ON GROWTH, PHOTOSYNTHESIS AND YIELD OF FOUR VARIETIES OF WHEAT

Akhmad Zubaidi[1,2], Gurjeet Gill[1] and Glenn K McDonald[1]

[1]School of Agriculture Food and Wine, The University of Adelaide
The University of Adelaide
Waite Campus
PMB 1 Glen Osmond, South Australia, 5054
AUSTRALIA
[2]Faculty of Agriculture, The University of Mataram, Indonesia



Statement of Authorship

Title of Paper	THE EFFECTSOF CONTINUOUSLY HIGH TEMPERATURES ON GROWTH AND YIELD OF FOUR VARIETIES OF WHEAT
Publication Status	○ Published, ○ Accepted for Publication, ○ Submitted for Publication, ● Publication style
Publication Details	

Author Contributions

By signing the Statement of Authorship, each author certifies that their stated contribution to the publication is accurate and that permission is granted for the publication to be included in the candidate's thesis.

Name of Principal Author (Candidate)	Akhmad Zubaidi		
Contribution to the Paper	Performed experiments, analysis on all samples, interpreted data, and wrote manuscript		
Signature		Date	24 - 11 - 2014

Name of Co-Author	Gurjeet Gill		
Contribution to the Paper	Helped to evaluate and edit the manuscript.		
Signature		Date	15 · 12 · 2014

Name of Co-Author	Glenn K McDonald		
Contribution to the Paper	Supervised development of work, data interpretation, manuscript evaluation and acted as corresponding author.		
Signature			15/12/14

Name of Co-Author			
Contribution to the Paper			
Signature		Date	

Abstract

Wheat is a temperate crop that recently has expanded into the low-latitude areas of the tropics where growing season temperatures are generally higher than those in the main wheat growing areas. Wheat growth and yield are sensitive to high temperatures, but much of the previous work has examined this effect at specific stages of development. However in tropical regions high temperature occurs throughout the growth cycle and is a major factor influencing growth and yield in this area. The aim of this work is to describe the responses to continuously-high temperatures on growth and yield of wheat under controlled conditions.

Two Indonesian wheat varieties (Nias and Dewata) and two Australian varieties (Axe and Gladius) were examined in growth room experiments at three different temperature regimes 32/23°C, 28/20°C, and 25/15°C day/night with 12 h daylight. Temperature and photoperiod were selected to simulate conditions on Lombok Island, at lowland (32/23°C) and highland (28/20°C) sites. The third temperature (25/15°C) was selected to represent temperature in a more temperate wheat-producing area.

High temperature reduced yield and dry matter accumulation which was associated with accelerated growth, a reduction in photosynthetic rate and stomatal conductance and an increase in respiration rate. The reduction in photosynthetic rate at high temperature was not only due to lower stomatal conductance but also to non-stomatal effects as mesophyll conductance and quantum yield were lower. Despite being exposed to high temperatures from establishment, the effect of high temperature was more severe during the reproductive stage as seen by the fact that yield was more affected than dry matter accumulation and yield was most strongly related to grain number. The accumulation of water soluble carbohydrates (WSC) was an important adaptive characteristic that was strongly associated with kernel weight and, to a lesser extent, grains per spikelet. Genetic variability in response to heat stress was evident with the Indonesian varieties being more

tolerant to high temperatures than Australian varieties. Nias and Dewata produced higher yield and biomass and maintaining higher rates of photosynthesis and remobilisation of WSC from vegetative tissues to grain. Maintaining high photosynthetic rate, high stomatal conductance, accumulation and remobilisation of WSC are important characters in adapting wheat into tropical environment such as Lombok Island.

1. Introduction

Wheat (*Triticum aestivum* L.) is a temperate cereal grown over a wide range of environments, but mostly in the range from 25° to 50° latitude. However, wheat production has expanded into tropical areas below 15° latitude (Badaruddin et al., 1999) where temperatures during the growing season are often much higher than those in the main wheat growing regions. In tropical environments wheat is grown during the cool season and often at high altitude to minimise the adverse effects of high temperature. Currently, the feasibility of growing tropical wheat in parts of Indonesia is being investigated as a means of diversifying cropping systems in response to predicted changes in climate (Kardono et al., 2012). Previous modelling work and field trials have demonstrated that yields in excess of 2 t/ha are possible (Gusmayanti et al., 2006; Handoko, 2007), including on Lombok Island in the eastern Indonesian archipelago and this was verified in recent field work on Lombok (Chapter 4). The potential growing season for wheat on Lombok is during the dry season after the main rice crop, from May to September. This would allow crops to flower in July,which is the coolest time of the year, with harvesting in August or early September, before the rainy season commences. However, during this time (May to September), mean temperatures are still high: 32°/23°C day/night at lowland sites and about 28°/20°C day/night at high elevations.

High temperature is a major environmental factor determining crop growth and yield (Blum, 1986; Alkhatib and Paulsen, 1990). The optimum temperature for wheat germination is less than 22°C (Slafer and Rawson, 1995), heading is 24.3°C (Slafer and Savin, 1991b), and for kernel growth 15°–20°C (Chowdhury and Wardlaw, 1978; Wardlaw and Moncur, 1995; Porter and Gawith, 1999). These optimum temperatures are all lower than those commonly experienced in tropical regions, including Lombok. In contrast to the traditional wheat-growing regions, where high temperature stress is generally more important during flowering and grain filling, in tropical regions high temperatures may persist for long periods of time commencing early in the growing season.

Research on heat stress in wheat is extensive, but the majority of the work has examined the effects of temperature at specific growth stages, and much of the work has focussed on the effects of terminal heat stress on grain set and grain filling (Shpiler and Blum, 1986; Stone and Nicolas, 1995b; Stone and Nicolas, 1995a; Wheeler et al., 1996a; Wardlaw, 2002; Mohammadi et al., 2004). Moreover, many of the experiments on heat stress under controlled conditions have used short-term heat stress events (Tashiro and Wardlaw, 1990; Acevedo et al., 1991; Stone and Nicolas, 1995b; Stone and Nicolas, 1995a; Wheeler et al., 1996a; Gibson and Paulsen, 1999; Porter and Gawith, 1999). There are few studies on plant growth and development in a continuous high temperature environment typical of the temperatures experienced in tropical regions and consequently the response to, and effect of this continuous high temperature on wheat yield are not well documented, or the few studies conducted have shown varying results. Rawson (1986) examined wheat yields under similar temperatures as those experienced on Lombok (30°/25°C) under controlled conditions and found significant variation in grain yield among a range of wheat varieties. The work demonstrated that high temperatures did not necessarily result in low grain set, a common feature of heat stress around flowering.

However, the field studies of Midmore et al. (1982) conducted at sites with a range of growing season temperatures found yield and a number of yield components were sensitive to high temperature. Recent field studies with wheat on Lombok have demonstrated that yield is sensitive to the differences in growing season temperature associated with altitude: yields increased by approximately 500 kg/ha for each 1°C fall in temperature associated with increases in altitude (Chapter 3). The field experiments on Lombok also found yield was more strongly related to grains/m^2 than to kernel weight, suggesting the effects of high temperature on pre-anthesis growth is more important to yield than post-anthesis growth.

The major limitations to wheat growth in the tropics are related to temperature, moisture and poor nutrition (Fischer, 1985; Wall, 1987), but heat stress is one of the common abiotic factors responsible for limiting production (Wardlaw et al., 1980). Yield reductions of wheat by high temperature are caused by several factors such as accelerated growth, increase in transpiration (Berry and Bjorkman, 1980) and reduction in net photosynthesis (Almeselmani et al., 2012). The effects of high temperature on growth and development of wheat has been widely reviewed (Wheeler et al., 1996a; Porter and Gawith, 1999). An increase in average daily temperature above 20-25°C hastens phenological development such as timing of double ridge, terminal spikelet initiation, and duration of spikelet primordial initiation as well time to flowering of wheat (Fischer and Maurer 1976; Slafer and Savin, 1991a; Slafer and Rawson, 1994), but further increases in temperature can delay development (Summerfield et al., 1991) (Chapter 4). Heat stress at specific growth stages can reduce yields significantly with the period just prior to and during flowering being especially sensitive (Fischer and Maurer, 1976). Increased sterility and reductions in kernel size can occur with even short exposures to high temperature around flowering (Saini and Aspinall, 1982; Talukder et al., 2013), and grain growth rates and final kernel weight are sensitive to temperatures above about 25ºC (Slafer and Rawson, 1995).

Biomass production is influenced by the development of leaf area and the rate of photosynthesis, both of which are sensitive to high temperatures. Leaf area can be reduced at high temperatures and high temperature also affects photosynthesis as well as other physiological processes such as respiration, stomatal conductance (g_s) and water relations (Taiz and Zeiger, 2002; Wahid et al., 2007), which in turn may affect crop biomass and yield (Fischer and Turner, 1978). Reduction of net photosynthesis and an increase in respiration under high temperature may be an important cause of low productivity of wheat in tropical environments. For example, the adaptability of plants to high temperatures has been found to be associated with the ability to maintain photosynthetic capacity (Pearcy, 1978).

Photosynthesis and remobilisation of stored water soluble carbohydrate (WSC) are the two major sources of carbon during grain filling period (McIntyre et al., 2011). WSC can make a significant contribution to final grain yield of about 10–20% under relatively non-stressed conditions (Gebbing et al., 1999) but post heading stress, when photosynthesis is reduced, increases the contribution of WSC to final yield to 50% or more (van Herwaarden et al., 1998; Rebetzke et al., 2008; Rattey et al., 2009). Therefore, remobilisation of WSC stored temporarily in the wheat stem helps to maintain the supply of carbon to the grain when the rate of photosynthetic production has declined (Blum et al., 1994; van Herwaarden et al., 1998). However, a significant proportion of the WSC stored in the stems accumulates prior to flowering and prolonged heat stress may limit the amount of WSC stored in the stem, limiting the ability of these stored reserves to buffer against environmental stress. Ruuska *et al.*, (2006) demonstrated that genetic variation exists for WSC accumulation in the stems at anthesis. The ability to accumulate WSC may therefore help plants adapt to high temperatures. It can probably be anticipated that the reductions in photosynthesis and the increases in respiration that occur under high temperatures will restrict the accumulation of WSC. However, little is known about the effects of prolonged exposure to high temperature on the concentrations of WSC in wheat or whether the levels of genetic variation reported under cooler temperatures is expressed under high temperatures.

High temperatures are a pervasive feature of the environment of tropical regions such as Lombok Island and although the effect can be alleviated by altitude, heat stress will be an important limitation to the productivity of wheat in this environment. The objectives of the current experiments were to develop a better understanding of wheat plant responses to prolonged high temperatures as a means of reducing the effects of heat stress on its growth and yield and improving the adaptation of wheat on Lombok Island. While there is no commercial wheat production in Indonesia, varieties of wheat have been developed in Indonesia and these may show some adaptation to high temperatures. In this experiment plants were grown under controlled conditions at temperatures to simulate low and high elevation locations on Lombok Island. Photosynthesis rates, water use and water use efficiency, WSC, growth and yield of 4 wheat genotypes (2 Australian and 2 Indonesian varieties) grown at 3 temperatures (32°/23°C, 28°/20ºC, and 25°/15ºC day/night) were compared. The work complemented field studies undertaken over two years on Lombok Island (Chapter4).

Materials and Methods

2.1 Plant material

Plant material consisted of 2 Australian (Axe and Gladius) and 2 Indonesian (Nias and Dewata) bread wheat varieties (*Triticum aestivum* L.).b bThey were chosen as they showed the most promising results in field experiments on Lombok and they represented a range in maturity types from early to mid-season (Chapter 4).

2.2. Experimental details

The experiment was conducted at the Waite Campus of the University of Adelaide, Australia. Plants were grown in pots (22cm in height and 25cm in diameter) filled with 6.0 kg of a standard fertile potting mix (coco peat soil).

The plants were grown in 3 different temperature regimes, 32°/23ºC, 28°/20°C, and 25°/15ºC day/night with 12 hours daylight, in 3 growth chambers, with 4 replications. Temperatures and photoperiod were selected to simulate conditions at sites on Lombok at low (32°/23ºC) and high (28°/20ºC) altitudes on the island. The lowest temperature (25°/15ºC) was selected to represent a temperature more typical of a wheat producing area in a temperate environment and was used as a low temperature control treatment. The temperatures and daylight treatments were maintained from germination to harvest. Light intensity in the growth rooms was 500-800 μmol quanta/m^2/s.

Seeds were sown in pots in December 2010 and harvested in March-April 2011. Six seeds were sown and thinned to 4 plants per pot once the seedlings had established. Pots were watered to their field capacity weight 2 or 3 times a week throughout the experiment, with more frequent watering in the highest temperature treatment, to avoid the occurrence of drought stress. The amount of water added was recorded. To monitor apical development of the varieties in each growth room 30 seeds of each variety were sown in a tray filled with the same potting mix and plant samples taken regularly for apical dissection.

2.3. Measurement of plant development and growth

Five seedlings were randomly selected from the trays two times per week, the main stem of each plant was dissected and the shoot apex was observed under a binocular dissecting microscope for stage of development and to record time of double ridge (DR) stage and terminal spikelet initiation (TSI). In the case when DR or TSI occurred between two successive observations, estimations were made between the two observations. At each observation the stage of development was recorded.

Plant samples were taken at anthesis, when the anthers emerged on the main stem (Zadoks growth stage (ZGS) 65; Zadoks et al. (1977)) and at maturity, when seeds were hard and the stems were yellow. One plant was randomly sampled from each pot at anthesis and the remaining 3 plants were sampled at maturity by cutting at soil level. At anthesis, plant samples were separated into leaf and stem, while at maturity the samples were separated into leaf, stem, and head. All samples were dried at 60°C for 48 hours and weighed. Leaf area at anthesis was measured by a Paton Electronic Planimeter. Yield was measured by weighing all the grains from all 3 plants in each pot. Yield components (spikelets per head, grain number per head and mean kernel weight) were also recorded. Water use efficiency based on total dry matter (WUE_{dm}) and grain yield (WUE_y) were calculated from total biomass and yield at maturity and the total water use over the course of the experiment.

2.4. Gas exchange measurements

A week after anthesis photosynthesis was measured on the flag leaf using a LI-6400 portable gas exchange system (LI-COR Inc., Lincoln NE, USA). This time was selected as representing a critical phase of crop development when grain set is determined and grain growth is commencing. Measurements were made between 9am and 1 pm. Two sets of measurements were made: a light response curve and a CO_2 response curve. Light intensity was set at 800 μmolm^{-2} s^{-1}with a red/blue light source for the CO_2 response curve and the CO_2 concentration was set at 400 μmol mol^{-1}for the light response curve. Leaf to air VPD was maintained at 1.1 kPa. The effect of temperature on non-stomatal control of photosynthetic capacity was analysed in two ways: by measuring CO_2 assimilation-intercellular CO_2 (*A:Ci*) response curves and by measuring light response curves. *A:Ci* response curves for individual leaves were obtained with a series of measurements, where *A* was initially measured after 10–15 min at ambient CO_2 (400 µmolmol^{-1}). To determine the initial slope of the *A:Ci* curve, the CO_2 concentration was gradually deceased to 0 µmol mol^{-1} (300, 200, 100, 30 and 0 µmol mol^{-1}). The CO_2concentration was then returned to 300 µmol mol^{-1}before progressively increasing it to 800 µmol mol^{-1} (300, 500, 600, 800 µmol mol^{-1}) to complete the curve. The light response curve was used to estimate the rate of mitochondrial respiration and the quantum efficiency of the plants at each temperature. The response curve was derived by measuring photosynthesis rates sequentially at light intensities of 2000, 1500, 1000, 500, 200, 100, 50, 25 and 0 µmole m^{-2} s^{-1} after 2 minutes equilibration at the new light intensity. The photosynthetic rate under zero light intensity was used as an estimate of mitochondrial respiration rate and the quantum efficiency was derived from the slope of the photosynthetic response between 0 and 100 µmole m^{-2} s^{-1}.

2.5. Measurement of water soluble carbohydrate

Dried whole stem samples from anthesis and maturity were ground in a Wiley mill to pass a 1-mm sieve. Carbohydrates were extracted from 0.1 g (ranged 0.100 to 0.110) of stem material by extracting at 80ºC with 8 ml of 80% ethanol (v/v) followed by extractions at 60ºC with 8 ml of distilled water. Water extractions were repeated twice. Extraction time was 60 min for each, after which tubes were centrifuged at room temperature for 10 minuteat 3400 rpm. Extracts were then combined. This procedure has been found to extract the soluble carbohydrates from plant tissue (Borrell et al., 1989; van Herwaarden et al., 1998). Total carbohydrates in the extract were analysed by the anthrone method of Yemm and Willis (1954) with fructose as a standard.

2.4. Experimental design and data analysis

The temperature treatments were conducted in separate growth rooms and therefore were unreplicated; these treatments were considered as separate growth environments and the data treated as a multi-environment analysis. At each temperature treatment (environment) the varieties were compared in a randomised complete block design with four replicates. The combined analysis treated Temperature as a fixed effect in the multi-environment analysis. The data were analysed with GenStat statistical package (VSN International Ltd, United Kingdom) by REML using the Multiple Experiments option. Temperature and Variety were considered as fixed effects. Relationships between variables were examined using correlations and regression analysis.

3. Results

3.1. Plant development

There were small effects of temperature on the time to DR and TSI but bigger differences were found in the time to flowering. Larger differences in rates of development generally occurred between 25°/15°C and 28°/20°C with relatively smaller differences between 32°/23°C and 28°/20°C. Plants grown at 25°/15°C were harvested 10-20 d later than those grown at 32°/23°C.

Times to DR and TSI in the two Australian varieties decreased (Axe) or were unaffected (Gladius) as temperature increased from 25°/15°C to 28°/20°C but in both varieties DR stage was delayed at 32°/23°C. However the early development of 2 Indonesian varieties was less sensitive to high temperature as their time to DR and TSI showed no significant difference at 28°/20°C and 32°/23°C. Flowering times spanned 15-20 days among the varieties at each temperature with Axe being the earliest and Dewata the latest (Table 5.1). Time to flower became shorter with higher temperatures in all varieties.

Table 5.1: Time taken to reach specific growth stages in four varieties of wheat grown at three temperatures. Values are shown as the mean ± standard error of the mean (n=4)

	Temperature (°C)		
	25/15	28/20	32/23
Double ridge			
Axe	17.2 ± 0.7	15.8 ± 0.2	17.5 ± 0.9
Gladius	21.8 ± 0.5	21.8 ± 0.8	26.8 ± 0.9
Nias	20.8 ± 0.2	20.2 ± 0.5	19.8 ± 0.5
Dewata	30.4 ± 0.4	30.2 ± 0.2	31.4 ± 0.2
Terminal Spikelet Initiation			
Axe	25.4 ± 0.4	22.2 ± 0.5	23.8 ± 0.8
Gladius	32.0 ± 0.0	31.2 ± 0.5	38.6 ± 0.4
Nias	34.4 ± 0.2	30.8 ± 0.5	29.6 ± 0.2
Dewata	41.6 ± 0.4	41.2 ± 0.5	40.4 ± 0.4
Anthesis (ZGS 65)			
Axe	56.0 ± 0.71	45.5 ± 0.50	44.3 ± 0.85
Gladius	70.5 ± 0.50	63.5 ± 0.65	61.0 ± 0.82
Nias	63.3 ± 0.48	53.3 ± 0.75	48.5 ± 0.65
Dewata	75.5 ± 0.29	71.8 ± 0.25	68.5 ± 0.50
Maturity			
Axe	115.3 ± 0.48	92.5 ± 0.29	93.8 ± 0.48
Gladius	129.5 ± 0.50	115.8 ±0.25	119.3 ± 0.75
Nias	118.3 ±0.48	102.3 ±0.48	97.3 ± 0.25
Dewata	127.5 ± 0.50	113.3 ± 3.61	107.5 ± 0.29

Table 5.2: Plant dry matter, stem weight, leaf weight and leaf area and specific leaf area (SLA) at anthesis

Temperature (°C)	Variety	Dry matter (g/plant)			Leaf area (cm^2/plant)	Leaf/stem ratio	SLA cm^2/g
		Total shoot	Stem	Leaf			
25/15	Axe	11.9	5.5	2.9	648	0.53	226
	Gladius	31.3	14.6	7.3	1427	0.50	199
	Nias	21.5	10.1	4.9	1133	0.49	234
	Dewata	25.5	12.5	7.6	1416	0.59	189
	Mean	22.6	10.7	5.6	1156	0.53	212
28/20	Axe	8.3	3.5	2.0	384	0.57	189
	Gladius	23.8	11.9	4.9	731	0.41	150
	Nias	13.0	4.9	2.4	470	0.48	196
	Dewata	22.2	8.2	4.9	697	0.58	146
	Mean	16.8	7.1	3.6	571	0.51	170
32/23	Axe	2.6	1.0	0.6	100	0.53	184
	Gladius	9.4	3.8	3.2	512	0.88	161
	Nias	10.4	3.7	2.0	304	0.52	153
	Dewata	14.8	5.4	3.6	334	0.66	102
	Mean	9.3	3.5	2.3	312	0.65	150
SED[A]	Temp	1.78	0.79	0.53	75.8	0.031	7.6
	Temp.Var	3.71	1.56	1.05	149.2	0.062	15.1
F-Probability							
	Temp	<0.001	<0.001	<0.001	<0.001	0.003	<0.001
	Temp.Var	<0.001	<0.001	<0.001	<0.001	0.004	<0.001

[A] Standard error of the difference among Temperatures and Varieties within each Temperature

3.2 Biomass production, yield and yield components

Time to maturity affected biomass production among the four varieties with the two early flowering varieties (Axe and Nias) producing significantly less biomass and smaller leaf areas than the later flowering varieties (Gladius and Dewata) at each temperature. Biomass accumulation was reduced when plants were grown at high temperatures. The average reduction as compared to the 25°/15°C control was 26% at 28°/20°C and 59% at 32°/23°C (Table 5.2), but varieties differed in their response. Dry matter at anthesis in the Australian varieties Axe and Gladius was affected more by high temperature than Nias and Dewata. When grown at 32°/23°C biomass of Axe was 78% lower and Gladius70% lower than the control, whereas the reductions were 52% in Nias and 42% in Dewata. At mild heat stress (28°/20°C) there was no clear difference between the Australian and Indonesian varieties.

Leaf and stem growth were reduced by higher temperature in all varieties as shown by decreased stem and leaf dry weight, as well as by leaf area. The leaf:stem ratio increased with high temperatures indicating that stem growth was affected more by high temperature than leaf growth. The exception was Axe where the ratio did not change. The biggest change occurred in Gladius. As the temperature increased, stem growth of Gladius was suppressed more than leaf growth, as shown by the higher leaf:stem ratio at 30°/23°C, but this did not occur in other cultivars (Table 5.2). Average leaf area showed a larger relative reduction (73%) compared to biomass (59%) at 30°/23°C. Consequently specific leaf area was reduced at the two higher temperatures (Table 5.2)

At maturity, Axe was the most affected by high temperatures with a decrease in dry matter at 32°/23°C of 87% compared to the control treatment, while the reduction among the other varieties ranged from 57% (Gladius and Dewata) to 65% (Nias) (Table 5.3).

All varieties produce similar yield when grown at the control temperature but yields were significantly lower at the two higher temperatures. At 28º/20ºC yields were 24% lower on average while they were 78% lower when grown at 32°/23°C although there was evidence of significant differences among the varieties in their response to high temperature. At 32º/23ºC the yield of Axe was reduced by 89% as compared to the control. Gladius and Dewata produced similar yields at 32º/23ºC but compared to their yields at 25°/15ºC, Gladius

Table 5.3: Plant yield and yield components of four wheat varieties grown under three temperature regimes.

Temp.	Variety	Total dry matter	Grain yield	Ears plant^{-1}	Spikelet ear^{-1}	Grains spikelet^{-1}	Grain number plant^{-1}	Kernel weight	HI
		(g/plant)						(mg)	(%)
25/15	Axe	37.9	16.2	14.1	12.9	3.2	590	29.1	42.9
	Gladius	48.0	16.7	16.6	13.7	2.6	568	29.8	34.8
	Nias	39.4	17.2	11.5	15.7	2.9	525	33.1	43.6
	Dewata	40.9	16.0	9.8	18.4	2.5	447	36.7	39.2
	Mean	41.5	16.5	13.0	15.2	2.8	532	32.2	40.1
28/20	Axe	26.2	11.3	15.3	11.1	2.6	402	28.1	42.7
	Gladius	42.6	14.6	24.8	12.5	1.7	542	27.2	34.3
	Nias	26.5	12.3	10.2	13.9	2.3	329	37.8	46.8
	Dewata	26.3	12.0	8.9	15.3	2.6	348	34.5	46.1
	Mean	30.4	12.6	14.8	13.2	2.3	405	31.9	42.5
32/23	Axe	5.1	1.8	5.3	8.8	1.6	74	24.2	36.7
	Gladius	20.6	3.0	18.5	12.6	0.5	120	23.9	13.6
	Nias	13.9	5.7	9.2	11.3	1.4	150	38.2	41.1
	Dewata	17.1	3.8	8.5	13.0	1.2	125	30.1	22.9
	Mean	14.2	3.6	10.4	11.4	1.2	117	29.1	28.6
	SED[A]								
	Temp	1.43	0.72	0.84	0.62	0.16	29.5	1.66	2.06
	Temp.Var	2.81	1.11	1.67	1.22	0.32	53.1	2.76	3.51
	F Prob								
	Temp	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	ns	<0.001
	Temp.Var	<0.001	0.003	<0.001	<0.001	0.003	0.006	<0.001	<0.001

[A] Standard error of the difference among Temperatures and among Varieties within each Temperature

was affected more (81% reduction) than Nias (67%) and Dewata (76%) (Table 5.3). The reduction in yield was associated with fewer grains per plant as well as lower kernel weight (Supplementary Fig.5.1). There was a consistent relationship between grain number and grain yield over all treatments and varieties (r=0.97, P<0.001, n= 12) while the relationship between grain yield and kernel weight was not significant when all the treatments were combined (r=0.43, ns). However when the relationship was examined at each temperature, differences in yield among the four varieties was associated with high kernel number (r=0.96, P<0.05, n=4) and kernel weight at 32°/23°C (r=0.93, P<0.05, n=4) but not at the other temperatures.

Across all treatments, grain number was most strongly associated with grains per spikelet (r=0.79, P=0.002, n=12) rather than ears per plant (r=0.44, ns) or spikelets per ear (r=0.47, ns), which indicates treatment effects on floret production and/or grain set were important determinants of yield. The sensitivity of grain set to high temperature was also reflected in the differences in HI. Values of HI were similar at 25º/15ºC and 28º/20ºC suggesting growth and yield were affected similarly, but the HI at 32º/23ºC was lower, indicating yield was affected more than dry matter production. The lowest HI in Gladius at 32º/23ºC was caused by low grain number/spikelet while ear number/plant was not affected (Table 5.3). There is also a strong relationship between grain yield and anthesis dry matter (r=0.72, P<0.01, n=12) indicating greater pre-anthesis vegetative growth was associated with greater yield.

3.3. Plant water use and water use efficiency

Total water use (WU) increased with higher temperaturesup to 28°/20ºC, but at 32°/23ºC, WU by Axe and Gladius decreased, especially in Axe. The larger reduction in WU by Axe was associated with a much reduced post-anthesis WU as the plants matured quickly. In contrast WU by the two Indonesian varieties did not decrease at the highest temperature (Fig 5.1). WUE_{dm} and WUE_{y} declined as temperature increased in all varieties (Fig 5.1). Among the four cultivars, Gladius used most water but there were no differences in WUE among varieties (Fig. 5.1).

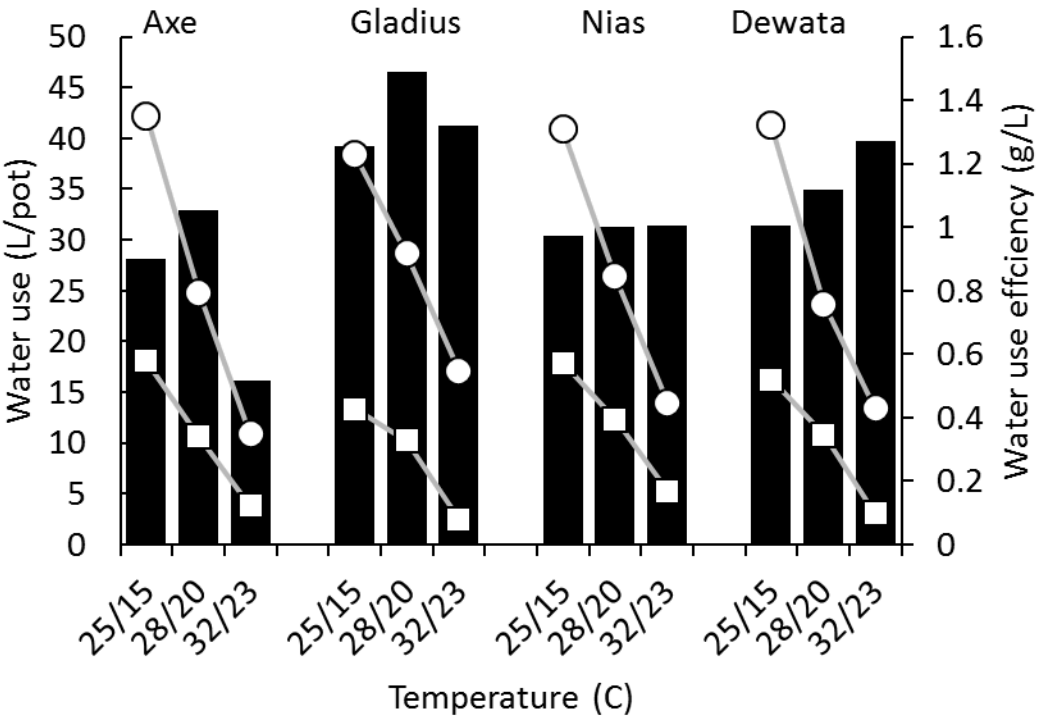


Figure 5.1 The effects of growth temperature on total water use (bars)and water use efficiency (lines) for dry matter production (○) and grain yield (□) for four varieties of wheat

3.4. Water Soluble Carbohydrate

Concentrations of WSC at anthesis and maturity of plants grown at 25º/15ºC were higher compared to plants grown at the two higher temperatures (Fig. 2). Within varieties, the two Indonesian varieties accumulated considerably more WSC at anthesis than the two Australian varieties.

WSC concentration fell markedly between anthesis and maturity with the relative reduction being higher at 28°/20°C except for Gladius. The two Australian varieties had a similar reduction in WSC (Axe: 45%; Gladius: 42%) which was less than that measured in the two Indonesian varieties (Nias: 76%; Dewata: 69%) (Fig. 5.2). Across all treatments,

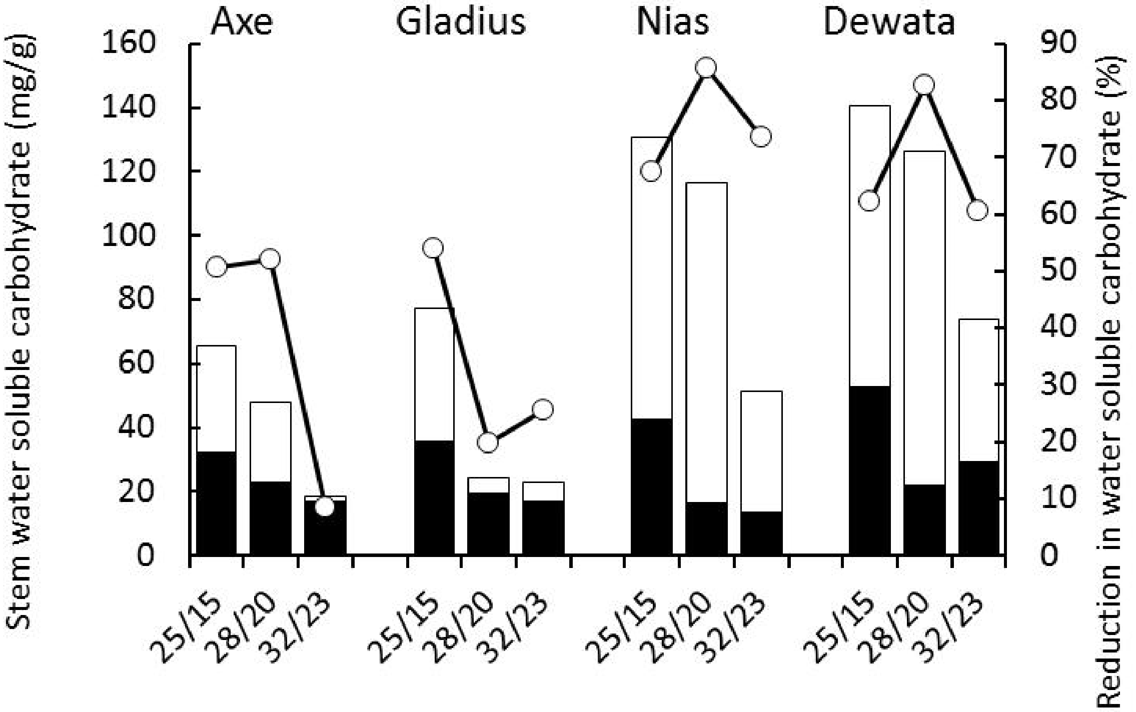


Fig 5.2. The concentrations of stem water soluble carbohydrate at anthesis (□) and maturity (■) and the percentage change between anthesis and maturity (lines) in four varieties of wheat grown at different temperatures

kernel weight was highly correlated with the concentration of WSC at anthesis (r=0.82, P<0.01, n=12) and the post-anthesis decline in WSC (r=0.87, P<0.001, n=12). The WSC concentration at anthesis was also weakly, but significantly correlated with grains per spikelet (r=0.59, P=0.042, n=12) but not with grain number per plant (r=0.36, ns).

3.4. Gas exchange measurements

Leaf temperatures were close to the air temperature with Nias showing a consistently lower temperature. At the two higher temperatures difference between air and leaf temperature was associated with a higher transpiration rate and stomatal conductance in this variety. Maximum photosynthetic rates declined with increased temperatures with the largest difference occurring between 28º/20ºC and 25º/15ºC (Supplementary Fig 5.2, Table 5.4). Stomatal conductance decreased with an increase in temperature and there were significant differences among varieties at each temperature. The Indonesian varieties maintained higher stomatal conductance at each temperature compared to Axe and Gladius and this was most evident at the two highest temperatures. This was reflected in higher values of Ci:Ca at 28º/20ºC and 32º/23ºC. Estimates of dark respiration showed small differences among the three temperatures and among varieties at each temperature, but at 28º/20ºC and 32º/23ºC Nias tended to have a slightly lower respiration rate compared to the other varieties (Table 5.4).

Quantum efficiency of photosynthesis declined with increasing temperatures in all the varieties except Gladius which showed little change, although its value was lower than the others at 25°/15°C which contributed to its stability (Table 5.5). Axe and Dewata, which showed the lowest photosynthetic rates at 32º/23ºC, had quantum efficiencies significantly lower than Gladius and Nias. Temperature affected the $A{:}C_i$ curves (Supplementary Figure 5.3). The initial slope of the $A{:}C_i$ curve estimates the RuBP-carboxylase-limited CO_2 fixation capacity of plants (Caemmerer and Farquhar, 1981; Seemann and Berry, 1982). At 32º/23ºC the lowest value was estimated for Dewata with no significant difference among the other varieties. Interestingly there was a consistent increase in CO_2 fixation at 28°/20°C in all varieties except Dewata (Table 5.5).

The reduction in photosynthetic rate with increasing temperatures was most strongly correlated with declines in stomatal conductance, apparent mesophyll resistance and quantum yield (Table 5.6). The reduction in mesophyll resistance was also associated with a lower initial slope of the CO_2 response curve.

Table 5.4: Leaf temperature (T_{leaf};°C), maximum rate of photosynthesis (A; μmol m^{-2} s^{2}),stomatal conductance ($g_{s;}$ mol m^{-2} s^{-2}), apparent mesophyll resistance (g_m), ratio of internal and external partial pressures of CO_2 (C_i:C_a), and dark respiration rate (R; μmol m^{-2} s^{-2})in four wheat varieties grown at three temperatures. Measurements were made on the flag leaf at anthesis

Treat	Variety	T_{leaf}	A	g_s	g_m	Ci:Ca	R
25/15	Axe	25.2	22.6	0.37	0.081	0.71	1.9
	Gladius	26.3	14.2	0.25	0.049	0.74	0.8
	Nias	24.9	25.1	0.65	0.080	0.81	1.8
	Dewata	25.1	22.7	0.41	0.079	0.74	2.2
	Mean	25.4	21.2	0.42	0.072	0.75	1.6
28/20	Axe	29.7	21.1	0.17	0.121	0.45	1.8
	Gladius	31.1	15.9	0.14	0.081	0.50	1.6
	Nias	28.8	21.9	0.33	0.081	0.70	1.3
	Dewata	29.4	18.9	0.42	0.064	0.77	1.9
	Mean	29.7	19.5	0.27	0.087	0.61	1.6
32/23	Axe	33.4	11.9	0.13	0.053	0.57	2.2
	Gladius	34.3	13.1	0.14	0.059	0.56	2.0
	Nias	28.2	16.9	0.32	0.065	0.73	1.7
	Dewata	33.4	8.1	0.22	0.025	0.81	2.4
	Mean	32.3	12.5	0.21	0.049	0.67	2.1
	SED[A]						
	Temp	0.24	1.08	0.027	0.0048	0.015	0.17
	Temp.Var	0.47	2.16	0.054	0.0096	0.030	0.33
	F Prob						
	Temp	<0.001	<0.001	<0.001	<0.001	<0.001	0.052
	Temp.Var	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

[A] Standard error of the difference among Temperatures and among Varieties within each Temperature

Table 5.5: The effects of temperature on the initial slope of the $A{:}C_i$ curve and the light response curve for four varieties of wheat grown at three temperatures. The values are shown as the mean ± s.e.m based on the regression at either external CO_2 concnetrations of 50, 100, 150 and 200 µmol mol^{-1} or light at 0, 25, 50 and 100 µmol m^{-2} s^{-1}. All regressions were significant ($P<0.001$)

Variety	Temperature		
	25°/15°	28°/20°	30°/23°
CO_2 response (x10^2)			
Axe	11.7 ± 0.04	28.4±1.20	8.8±0.74
Gladius	6.1 ± 0.30	15.0 ± 0.59	9.4 ± 0.47
Nias	9.1 ± 0.62	11.8 ± 1.00	8.5 ± 0.69
Dewata	10.8 ± 0.70	7.8 ± 0.41	5.7 ± 0.08
Light response (x10^3)			
Axe	5.2± 0.20	5.0±0.21	3.6± 0.23
Gladius	4.4± 0.07	4.3± 0.21	4.2± 0.08
Nias	5.4± 0.16	4.0± 0.07	4.2± 0.44
Dewata	5.4± 0.03	4.4± 0.15	3.6± 0.21

The effects of temperature on photosynthesis and leaf conductance were also reflective of the variation in whole plant growth. Dry matter production at maturity was correlated with quantum efficiency and weakly, but significantly, with mesophyll resistance while grain yield was significantly correlated with photosynthetic rate, stomatal conductance and quantum efficiency (Table 5.6).

4. Discussion

Heat stress is a major problem in adapting wheat to tropical areas. The aim of the experiment was to examine how wheat responded to extended periods of high temperatures under controlled conditions to supplement field studies with these varieties on Lombok Island. When the results from this experiment are compared with results from field

Table 5.6. Correlation coefficients between grain yield, biomass at anthesis (DMa), biomass at maturity (DMm), time to anthesis, specific leaf area (SLA), stem water soluble carbohydrate at anthesis (WSCa), photosynthetic rate (A), stomatal conductance (gs), the ratio of internal and external partial pressures of CO_2 (Ci:Ca), estimate of mesophyll resistance (g_m), quantum efficiency (QE), initial response to CO_2 curve (CO_2 resp) and estimate of mitochondrial respiration (R) among four varieties of wheat grown at three temperatures (n=12). Significance levels are shown as: * P<0.05; ** P<0.01; *** P<0.001

	Yield	DMa	DMm	Anthesis	SLA	WSCa	A	gs	Ci:Ca	g_m	QE	CO_2 resp	R
Yield	1.00												
DMa	0.72**	1.00											
DMm	0.87***	0.64*	1.00										
Anthesis	0.41	0.84***	0.36	1.00									
SLA	0.60*	0.07	0.48	-0.20	1.00								
WSCa	0.58*	0.54	0.30	0.56	0.27	1.00							
A	0.73**	0.19	0.55	-0.02	0.73**	0.60*	1.00						
g_s	0.58*	0.39	0.25	0.35	0.48	0.83***	0.71*	1.00					
Ci:Ca	0.24	0.42	-0.09	0.54	0.02	0.72**	0.12	0.72**	1.00				
g_m	0.48	-0.08	0.59*	-0.34	0.54	0.09	0.76**	0.14	-0.51	1.00			
QE	0.74**	0.36	0.73**	0.23	0.67*	0.48	0.83***	0.62*	0.10	0.65*	1.00		
CO_2res	0.17	-0.28	0.45	-0.47	0.20	-0.23	0.38	-0.26	-0.73**	0.87***	0.35	1.00	
R	-0.49	-0.45	-0.47	-0.01	-0.36	-0.07	-0.18	-0.03	0.01	-0.16	-0.04	-0.03	1.00

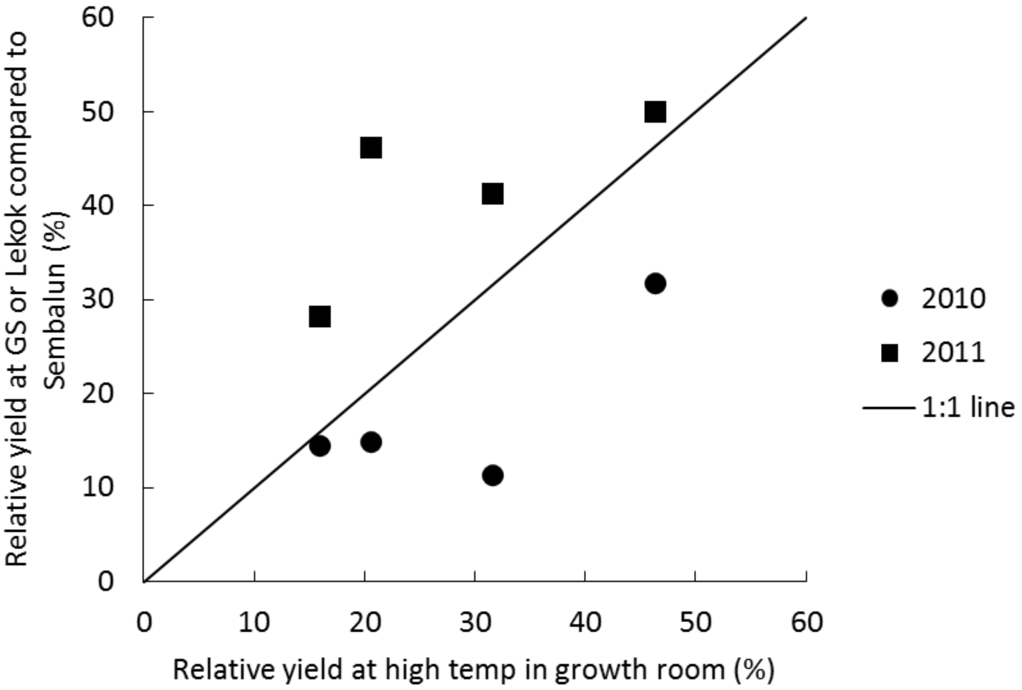


Fig 5.3: The relationship between sensitivity in yield to high temperature among four wheat varieties when grown in the field or in growth rooms. The relative yields from the field trials are derived from experiments on Lombok at warm lowland sites (Gunung Sari in 2011 or Lekok in 2012) and at a cool highland site (Sembalun) in 2011 and 2012 and the relative yields in the growth rooms are based on growth at 32°/23°C and 28°/20°C.

experiments conducted over two seasons on Lombok Island (Fig 5.3), there is general agreement in the relative ranking in sensitivities among the four varieties to high temperature, although the relative yields under high temperature in the field trials differed between the years. A possible reason for the smaller effect of high temperatures in the field is discussed below; nevertheless the comparison suggests that the relative sensitivities in yield to high temperature among the four varieties measured in the present experiment relate to those observed in the field.

4.1 Plant development

Continuous high temperature in the tropics may affect seed germination and establishment during early growth and by its adverse effects on leaf area development and net photosynthesis, it can reduce biomass production (Wahid et al., 2007). The rate of plant development increases with high temperature up to an optimum temperature after which development slows with further increases in temperatures (Summerfield et al., 1991). This effect was apparent in the present experiments though there were differences among varieties investigated. Times to DR and TSI were little affected or reduced when the growth temperature was raised to 28°/20°C but they were delayed by 1.5-5 d (DR) or by 1.5-7 d (TSI) at 32°/23°C in the two Australian varieties. Based on its greater response in time to DR and TSI, the early development of Gladius seems to be relatively more sensitive to high temperature than the other varieties. The optimum temperature for early development is around 21°C (Slafer and Rawson, 1995) and delays in DR and TSI with higher temperatures and genetic differences in sensitivity to high temperature have been reported previously (Rawson and Richards, 1992). It is notable that the rates of development of the Indonesian varieties, which presumably were developed for warm climates, appear to be less sensitive to high temperatures at these early stages. The response in flowering time differed from that observed with DR and TSI: time to flower became progressively shorter with higher temperatures in all varieties up to 32°/23°C and the Indonesian varieties were equally sensitive as the Australian varieties. It has been shown by Slafer and Rawson (1995) that the optimum temperaturefor development increases in later growth stages and the fact that time to flower is not delayed at the highest temperature is consistent with a higher optimum temperature for development after the DR stage.

The growth room experiment was designed to mimic the temperature effects at a high temperature lowland site and a low temperature highland site on Lombok Island.

However, the results in this experiment are different from a field experiment on Lombok 2010, in which the early apical development at a lowland site (mean growing season temperature = 32°/23°C), was 1-3 days quicker than at an upland site (mean growing season temperature = 28°/20°C) (Chapter 3). While the average maximum and minimum temperatures were similar in the field experiments and in the growth room, plants in the growth room were exposed to 32°C for 12 hours whereas in the field the natural diurnal variation in temperature meant that the maximum temperature occurred over a shorter period of time (about 4-6 h). This difference in exposure to the high temperatures during the day between the growth room and the field may have amplified the effect of high temperature on early development in the growth room.

High temperature reduced the time to anthesis, which was related to a reduction in yield (Fig 5.4a). The relationships for the two early varieties (Axe and Nias) and the two later varieties (Gladius and Dewata) differed. The reduced yield was also associated with a reduction in the time between TSI and anthesis (Fig 5.4b). There was no association between yield and time to DR or TSI (data not shown). The time from TSI to anthesis includes the period of floret development and the relationship observed in Fig 5.4b is consistent with the importance of grain number and grains per spikelet to yield observed in this experiment as well as in the field experiments (Chapter 4). Therefore, varieties with a longer period of ear development, including time from TSI to anthesis, or more stress-tolerant varieties, which maintain the length ear development period, could be used to increase grain yield. However this strategy may be limited at very high temperatures: the largest reduction in yield and grain number generally occurred between 28°/20°C and 32°/23°C, when there was a relatively small change in the duration of the TSI-anthesis period. While rate of development

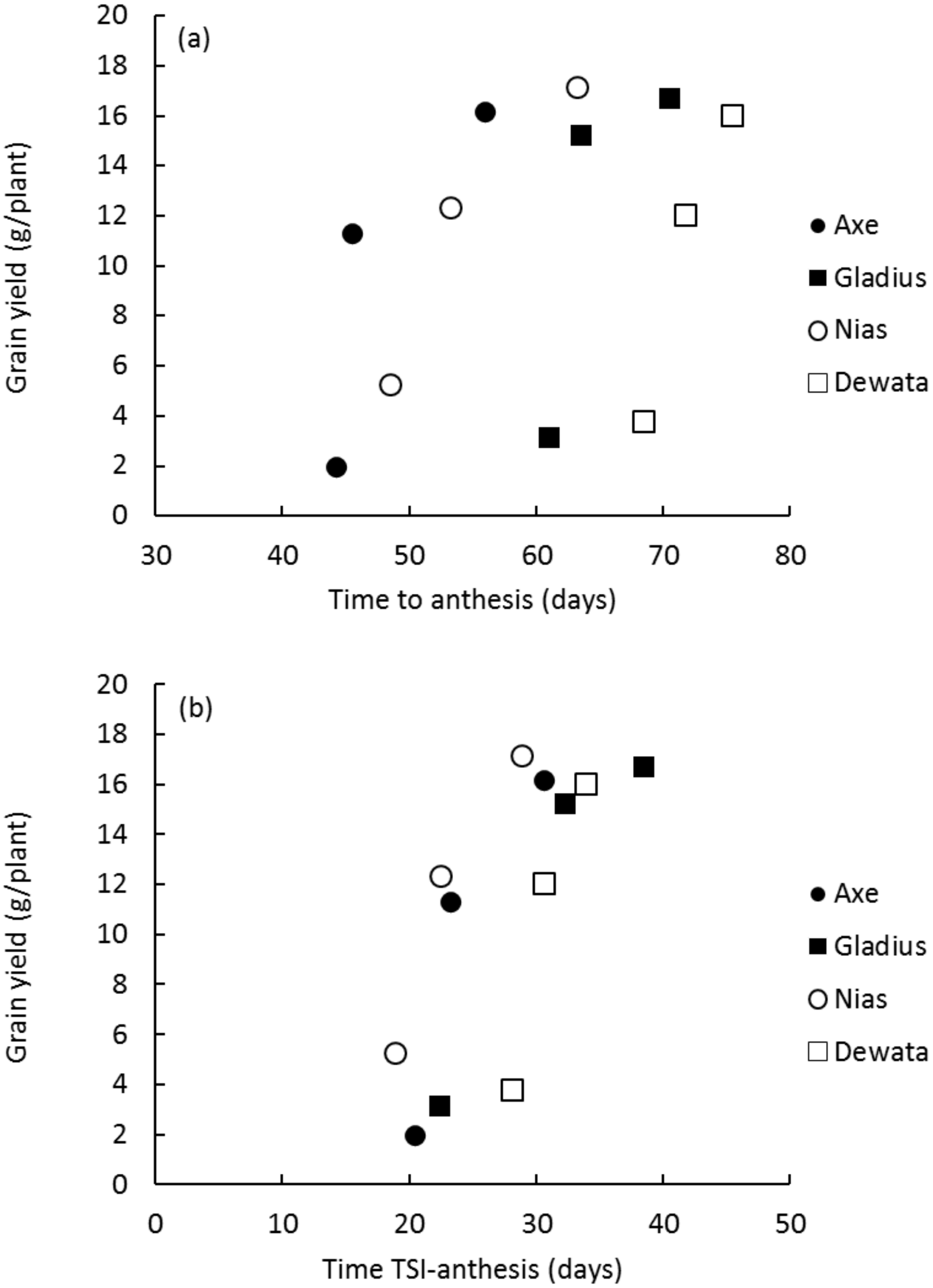


Fig.5.4. The relationship between time to anthesis (a) and time TSI-anthesis (b) to yield of 4 varieties tested.

is an important influence on yield, at very high temperatures heat stress appears to become an overriding factor.

4.2 Variation in response to high temperature among varieties

High temperature reduced most measures of growth and yield, but there was evidence of genetic variation in sensitivity to high temperature. All varieties showed a large reduction in yield when grown at 32/23°C, but the two Indonesian varieties showed smaller yield losses than the Australian varieties. The yields of Nias and Dewata at 32°/23°C were higher than those of Axe and Gladius and the reduction in yields were less: grain yields of Axe and Gladius were 89% and 82% lower respectively at 32°/23°C compared to the control temperature, while the yield losses of Nias and Dewata were 67% and 76% respectively. Compared to the Australian varieties, Nias and Dewata at 32°/23°C produced more biomass at flowering and showed smaller relative losses in biomass relative to the control, had higher concentrations and greater remobilisation of WSC, higher stomatal conductance, produced heavier kernels and maintained ear numbers better. These results suggest the two Indonesian varieties may possess inherently higher levels of heat tolerance compared to the two Australian varieties. Nias in particular possessed a number of traits that suggested it is more tolerant to high temperature compared to the other varieties. It produced higher biomass at high temperatures and showed the greatest reduction of WSC between anthesis and maturity suggesting it transfers more soluble carbohydrate to the grains than the other varieties, as well as maintaining the highest photosynthetic rate and stomatal conductance at high temperature. However the greater apparent thermotolerance of Nias and Dewata was not directly associated with an ability to maintain photosynthesis as the photosynthetic rate of Dewata was much reduced at 32°/23°C. Compared to Nias, stomatal conductance in Dewata was lower and the Ci:Ca ratio higher, suggesting there were non-stomatal limitations to photosynthesis. The decline in quantum yield and in the initial slope of the Ci:Ca curve indicates disruption of chloroplast activity which was not observed in Nias.

In contrast to Nias, the early maturing variety Axe showed the greatest yield loss at the highest temperature which was associated with large reductions in ear number and grain number/plant as well as low leaf area and biomass at anthesis. Along with Dewata, Axe recorded the lowest rate of photosynthesis and quantum yield at 32°/23°C. In more temperate environments such as the southern Australian cereal zone, where the environment is characterised by rising temperatures during spring, early flowering in Axe helps it to escape high temperature stress late in the season, so it generally may not have to cope with heat stress as much as later season varieties such as Gladius. However in a tropical environment where plants are exposed to high temperatures throughout their life-cycle, low tolerance to heat and fast development in Axe caused low dry matter accumulation and resulted in a low yield. While it's quick development would have contributed to its low biomass production at high temperature, its low leaf area and low rate of photosynthesis would have limited total photosynthesis at high temperature.

Pre- and post anthesis effects

At 32°/23°C grain yield was affected more than dry matter, which caused HI to decline. Both grain number and kernel weight were reduced as temperature increased but correlation analysis showed that grain number per plant was more important for yield across all the treatments and varieties (Table 5.3, Supplementary Fig. 5.1). The major influence on grains per plant was grains per spikelet. The development of sink capacity within the ear and grain set appeared to be crucial factors in determining the response of wheat varieties grown under continuous high temperature. This result is similar to previous studies in which plants were exposed to shorter periods of heat stress around flowering (Fischer and Maurer, 1976; Tashiro and Wardlaw, 1990; Stone and Nicolas, 1995b). High temperatures during floral initiation and spikelet development, a period of several weeks before anthesis, can reduce floret development and survival and limit the number of grains that determine yield potential (Calderini et al., 2001). This is associated with a shorter duration of floret development which may not only limit the number of spikelets and florets formed, but also reduce grain set, as temperatures above 30°C during floret formation have been shown to cause complete sterility (Saini and Aspinall, 1982). This is evident in the experiment by the significant reduction in the number of grains/spikelet at 30°/23°C (Table 5.3) and the importance of the period between TSI and anthesis to yield (Fig 4b).

There were also significant reductions in grain weight at 32°/23°C and yield at this temperature among the four varieties was significantly correlated with kernel weight. These relationships were not evident at 28°/20° C. Previous studies have shown that the optimum temperature of grain filling is approximately 15-18°C and reductions in grain weight are primarily due to reductions in the duration of grain filling and in starch synthesis in the developing grain (Jenner, 1991; Stone and Nicolas, 1995a; Stone and Nicolas, 1995b; Wheeler et al., 1996a). As temperatures increase above the optimum, the initial change in grain weight can be small because the reduced duration of grain growth can be partially compensated by the increase in the rate of grain filling (Nicolas et al., 1984; Hunt et al., 1991; Jenner, 1991; Wheeler et al., 1996b). As temperatures increase further, the duration of grain filling continues to decline resulting in smaller grain at maturity (Shpiler and Blum, 1986; Tashiro and Wardlaw, 1990; Wardlaw, 2002).

Remobilisation of WSC stored temporarily in the wheat stem helps to maintain the supply of carbon to the grain when the rate of photosynthetic production has declined (Blum et al., 1994; van Herwaarden et al., 1998; McIntyre et al., 2011) and this was found to be an important trait in the present experiment: grain weight was related to the differences in WSC at anthesis and remobilisation during grain filling and this was reflected in the significant relationship between yield and WSC concentration at anthesis among the different temperatures (Table 5.6). Variation in the concentration of WSC was more important in influencing kernel weight than grain number, suggesting that the greater value of WSC was on post anthesis growth in these experiments. However the observation that WSC concentration was positively correlated with grains/spikelet shows that stem WSC may be associated with the growth of the developing ear and to fertility.

Variation in WSC at anthesis was associated with the variation in photosynthesic rates at anthesis but was not related to the respiration rate, suggesting that assimlation rate had a greater influence on the accumulation of reserves of WSC (Table 5.6). There was a wide variation in WSC among the four varieties with the two Indonesian varieties showing considerably higher concentrations than the Australian varieties. The ability to accumualte WSC in the stems appears to be an important adaptive characteristic of wheat varieties growing in temperatures typical of the tropical environment of Lombok to maintain grain set and especially grain growth.

Photosynthesis and whole plant growth

It is known that high temperature may induce stomatal closure and reduce photosynthesis (Berry and Bjorkman, 1980; Gutierrez-Rodriguez et al., 2000; Almeselmani et al., 2012). Measurements of the photosynthetic rates of flag leaves at anthesis showed a substantial decline at 32°/23°C compared to 20°/15°C, but relatively little reduction at 28/20°C. Tolerance to moderate to high temperatures has been reported in other temperate crops; for example Haldiman and Feller (2005) found photosynthetic rates of mature pea leaves changed by less than 10% when exposed to temperatures between 25°C and 35°C. The reduction in photosynthetic rate at 32/23°C was due to stomatal and non-stomatal effects because the stomatal conductance and mesophyll resistance (Table 5.5) and quantum yield (Table 5.6) were lower.

While it is often difficult to demonstrate a direct effect of leaf photosynthetic rates on whole plant growth and yield, in this experiment differences in photosynthetic rates measured at anthesis were significantly correlated with observed difference in yield. Previous field studies in both warm and temperate environments have also found that differences in yield among varieties can be related to differences in photosynthetic rates and in stomatal conductance (Fischer et al., 1998; Gutiérrez-Rodríguez et al., 2000; Reynolds et al., 2000) and similar trends were observed in the current experiment, although the relationships were largely due to the growth environment rather than varieties. However at 32°/23°C it is notable that Nias maintained a high yield relative to the other varieties which was associated with a high stomatal conductance and photosynthetic rate. High photosynthetic rates also contributed to the storage of WSC and ultimately to kernel weight.

5. Conclusion

High temperature reduced yield and dry matter accumulation of wheat which are caused by accelerated growth, reduced grain set, reduction in photosynthetic rate, and stomatal conductance. The effect of high temperature is more severe during there productive stage as seen by the fact that yield is affected more than dry matter accumulation. Moreover the number of grains/plant which reflects grain set is strongly correlated with yield and this was related to the duration of the period of spikelet development. Even though the growing season in the field on Lombok is short (approximately 120 days), early flowering varieties may not be beneficial unless they show a high level of heat tolerance. The heat escape mechanism associated with early flowering, which may be useful in Mediterranean environments, is not suitable for tropical environments where heat stress is pervasive during the whole growing season. In this study, the early flowering variety Axe showed a rapid rate of development and low biomass accumulation which also limited its yield potential.

There was some evidence of genetic variability to heat stress in this experiment. The differences in yield among varieties at high temperature was related to differences in photosynthetic rate, stomatal conductance as well as the amount and remobilisation of WSC. The Indonesian varieties were more tolerant to high temperature than Australian varieties. These traits could be used to select wheat varieties better adapted to high temperature tropical environments such as Lombok.

References

Acevedo, E., Nachit, M., Ortis-Ferrara, G., 1991. Effect of heat stress on wheat and possible selection tools for use in breebing for tolerance. Wheat for the nontraditional warm areas; Proceeding of an International Conference, Foz do Iguacu, Brazil, pp. 401-421.

Alkhatib, K., Paulsen, G.M., 1990. Photosynthesis and Productivity during High-Temperature Stress of Wheat Genotypes from Major World Regions. Crop Science 30, 1127-1132.

Almeselmani, M., Deshmukh, P.S., Chinnusamy, V., 2012. Effect of prolonged high temperature stress on respiration, photosynthesis and gene expression in wheat (*Triticum aestivum* L.) varieties differing in their thermotolerance. Plant Stress 6, 25-32.

Badaruddin, M., Reynolds, M.P., Ageeb, O.A.A., 1999. Wheat management in warm environments: effect of organic and inorganic fertilizers, irrigation frequency, and mulching. Agronomy Journal 91, 975-983.

Berry, J., Bjorkman, O., 1980. Photosynthetic Response and Adaptation to Temperature in Higher Plants. Annual Review of Plant Physiology and Plant Molecular Biology 31, 491-543.

Blum, A., 1986. The Effect of Heat Stress on Wheat Leaf and Ear Photosynthesis. Journal of Experimental Botany 37, 111-118.

Blum, A., Sinmena, B., Mayer, J., Golan, G., Shpiler, L., 1994. Stem Reserve Mobilisation Supports Wheat-Grain Filling Under Heat Stress. Australian Journal of Plant Physiology 21, 771-781.

Borrell, A.K., Incoll, L.D., Simpson, R.J., Dalling, M.J., 1989. Partitioning of dry matter and the deposition and use of stem reserves in a semi-dwarf wheat crop. . Annals of Botany 63, 527-539.

Caemmerer, S., Farquhar, G.D., 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153, 376-387.

Calderini, D.F., Savin, R., Abeledo, L.G., Reynolds, M.P., Slafer, G.A., 2001. The importance of the period immediately preceding anthesis for grain weight determination in wheat. Euphytica 119, 199-204.

Chowdhury, S.I., Wardlaw, I.F., 1978. The effect of temperature on kernel development in cereals. Australian Journal of Agricultural Research 29, 205-223.

Fischer, R.A., 1985. Physiological limitations to producing wheat in semitropical and tropical environments and possible selection criteria. Wheats for more tropical environments. A proceedings of an international symposium on wheat production and research in tropical environments, held in Mexico on 24-28 September, 1984. CIMMYT, Mexico, pp. 209-230.

Fischer, R.A., Maurer O, R., 1976. Crop temperature modification and yield potential in a dwarf spring wheat. Crop Science 16, 855-859.

Fischer, R.A., Rees, D., Sayre, K.D., Lu, Z.M., Condon, A.G., Saavedra, A.L., 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. Crop Science 38, 1467-1475.

Fischer, R.A., Turner, N.C., 1978. Plant productivity in the arid and semiarid zones. Annual Review of Plant Physiology 29, 277-317.

Gebbing, T., Schnyder, H., Kuhbauch, W., 1999. The utilization of pre-anthesis reserves in grain filling of wheat. Assessment by steady-state (CO2)-C-13/(CO2)-C-12 labelling. Plant Cell and Environment 22, 851-858.

Gibson, L.R., Paulsen, G.M., 1999. Yield components of wheat grown under high temperature stress during reproductive growth. Crop Science 39, 1841-1846.

Gusmayanti, E., Pertiwi, S., Handoko, Risdiyanto, I., Machida, T., 2006. Determining potential wheat growing areas in Indonesia by using the spatial compromise programming technique. Agricultural Information Research 15, 373-379.

Gutierrez-Rodriguez, M., Reynolds, M., Larque-Saavedra, A., 2000. Photosynthesis of wheat in a warm, irrigated environment - II. Traits associated with genetic gains in yield. Field Crop Research 66, 51-62.

Haldimann, P., Feller, U., 2005. Growth at moderately elevated temperatures alters the physiological response of the photosynthetic apparatus to heat stress in pea (*Pisum sativum* L.) leaves. Plant Cell and Environment 28, 302-317.

Handoko, I., 2007. Gandum 2000: Penelitian Pengembangan Gandum di Indonesia. SEAMEO BIOTROP, Jakarta.

Hunt, L.A., Poorten, G.v.d., Pararajasingham, S., 1991. Postanthesis temperature effects on duration and rate of grain filling in some winter and spring wheats. Canadian Journal of Plant Science 71, 609-617.

Jenner, C.F., 1991. Effects of exposure of wheat ears to high temperature on dry matter accumulation and carbohydrate metabolism in the grain of two cultivars. I. Immediate responses. Australian Journal of Plant Physiology 18, 165-177.

Kardono, Widiatmini Sih Winan, Agung Riyadi, Purwanta, W., 2012. Indonesia's technology needs assessment for climate change adaptations 2012. National Council on Climate Change of Indonesia, Jakarta, p. 183.

McIntyre, C.L., Casu, R.E., Rattey, A., Dreccer, M.F., Kam, J.W., van Herwaarden, A.F., Shorter, R., Xue, G.P., 2011. Linked gene networks involved in nitrogen and carbon metabolism and levels of water-soluble carbohydrate accumulation in wheat stems. Functional & Integrative Genomics 11, 585-597.

Midmore, D.J., Cartwright, P.M., Fischer, R.A., 1982. Wheat in tropical environments. I. Phasic development and spike size. Field Crops Research 5, 185-200.

Mohammadi, V., Qannadha, M.R., Zali, A.A., Yazdi-Samadi, B., 2004. Effects of post-anthesis heat stress on the head traits of wheat. International Journal of Agriculture and Biology 6, 42-44.

Nicolas, M.E., Gleadow, R.M., Dalling, M.J., 1984. Effects of drought and high temperature on grain growth in wheat. Australian Journal of Plant Physiology 11, 553-566.

Pearcy, R.W., 1978. Effect of growth temperature on the fatty acid composition of the leaf lipid in *Artiflex lentiformis* (Torr.) wats. Plant Physiology 59, 873-878.

Porter, J.R., Gawith, M., 1999. Temperatures and the growth and development of wheat: a review. European Journal of Agronomy 10, 23-36.

Rattey, A., Shorter, R., Chapman, S., Dreccer, F., van Herwaarden, A., 2009. Variation for and relationships among biomass and grain yield component traits conferring improved yield and grain weight in an elite wheat population grown in variable yield environments. Crop & Pasture Science 60, 717-729.

Rawson, H.M., 1986. High temperature tolerance in wheat: a description of variation and a search for some limitations to productivity. Field Crops Research 14, 197-212.

Rawson, H.M., Richards, R.A., 1992. Effects of high temperature and photoperiod on floral development in wheat isolines differing in vernalisation and photoperiod genes. Field Crops Research 32, 181-192.

Rebetzke, G.J., van Herwaarden, A.F., Jenkins, C., Weiss, M., Lewis, D., Ruuska, S., Tabe, L., Fettell, N.A., Richards, R.A., 2008. Quantitative trait loci for water-soluble carbohydrates and associations with agronomic traits in wheat. Australian Journal of Agricultural Research 59, 891-905.

Reynolds, M.P., Delgado B, M.I., Gutiérrez-Rodrı́guez, M., Larqué-Saavedra, A., 2000. Photosynthesis of wheat in a warm, irrigated environment: I: Genetic diversity and crop productivity. Field Crops Research 66, 37-50.

Ruuska, S.A., Rebetzke, G.J., van Herwaarden, A.F., Richards, R.A., Fettell, N.A., Tabe, L., Jenkins, C.L.D., 2006. Genotypic variation in water-soluble carbohydrate accumulation in wheat. Functional Plant Biology 33, 799-809.

Saini, H.S., Aspinall, D., 1982. Sterility in wheat (Triticum aestivum L.) induced by water deficit or high temperature: possible mediation by abscisic acid. Australian Journal of Plant Physiology 9, 529-537.

Seemann, J.R., Berry, J.A., 1982. Interspecific differences in the kinetic properties of RuBP carboxylase protein. Carnegie Inst. Washington Year Book 81, 78-83.

Shpiler, L., Blum, A., 1986. Differential reaction of wheat cultivars to hot environments. Euphytica 35, 483-492.

Slafer, G.A., Rawson, H.M., 1994. Sensitivity of wheat phasic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. Australian Journal of Plant Physiology 21, 393-426.

Slafer, G.A., Rawson, H.M., 1995. Rates and cardinal temperatures for processes of development in wheat: effects of temperature and thermal amplitude. Aust. J. Plant Physiol 22, 913-926.

Slafer, G.A., Savin, R., 1991a. Developmental base temperature in different phenological phases of wheat (triticum-aestivum). Journal of Experimental Botany 42, 1077-1082.

Slafer, G.A., Savin, R., 1991b. Developmental base temperature in different phenological phases of wheat (*Triticum aestivum* L.). Journal of Experimental Botany 42, 1077-1082.

Stone, P.J., Nicolas, M.E., 1995a. Effect of timing of heat stress during grain filling on two wheat varieties differing in heat tolerance .1. Grain growth. Australian Journal of Plant Physiology 22, 927-934.

Stone, P.J., Nicolas, M.E., 1995b. A survey of the effects of high temperature during grain filling on yield and quality of 75 cultivars of wheat. Australian Journal of Agricultural Research 46, 475-492.

Summerfield, R.J., Roberts, E.H., Ellis, R.H., Lawn, R.J., 1991. Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. Experimental Agriculture 27, 11-31.

Taiz, L., Zeiger, E., 2002. Plant Physiology. Sinaeur Associates, Inc., Publishers, Sunderland, Massachusetts.

Talukder, A.S.M.H.M., McDonald, G.K., Gill, G., 2013. Effect of short-term heat stress prior to flowering and at early grain set on the utilization of water-soluble carbohydrate by wheat genotypes. Field Crops Research.

Tashiro, T., Wardlaw, I.F., 1990. The response to high temperature shock and humidity changes prior to and during the early stages of grain development in wheat. Australian Journal of Plant Physiology 17, 551-561.

van Herwaarden, A.F., Angus, J.F., Richards, R.A., Farquhar, G.D., 1998. 'Haying-off', the negative grain yield response of dryland wheat to nitrogen fertiliser - II. Carbohydrate and protein dynamics. Australian Journal of Agricultural Research 49, 1083-1093.

Wahid, A., Gelani, S., Ashraf, M., Foolad, M.R., 2007. Heat tolerance in plants: an overview. Environmental and Experimental Botany 61, 199-223.

Wall, P.C., 1987. Central and South America. In: Klatt, A.R. (Ed.), Wheat production constraints in tropical environments. CIMMYT, Mexico, pp. 27-36.

Wardlaw, I.F., 2002. Interaction between drought and chronic high temperature during kernel filling in wheat in a controlled environment. Annals of Botany 90, 469-476.

Wardlaw, I.F., Moncur, L., 1995. The response of wheat to high temperature following anthesis. I. The rate and duration of kernel filling. Australian Journal of Plant Physiology 22, 391-397.

Wardlaw, I.F., Sofield, I., Cartwright, P.M., 1980. Factors Limiting the Rate of Dry Matter Accumulation in the Grain of Wheat Grown at High Temperature. Functional Plant Biology 7, 387-400.

Wheeler, T.R., Hong, H.D., Ellis, R.H., Batts, G.R., Morison, J.I.L., Hadley, P., 1996a. The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L) in response to temperature and CO_2. Journal of Experimental Botany 47, 623-630.

Wheeler, T.R., Hong, T.D., Ellis, R.H., Batts, G.R., Morison, J.I.L., Hadley, P., 1996b. The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO 2. Journal of Experimental Botany 47, 623-630.

Yemm, E.W., Willis, A.J., 1954. The estimation of carbohydrates in plant extracts by anthrone. The Biochemical Journal 57, 508-514.

Zadoks, J.C., Chang, T.T., Konzak, C.F., 1977. A decimal code for stages in the development of cereals (Un code decimal pour les stades de croissance des cereales). Phytiatrie-Phytopharmacie 26, 129-140.

CHAPTER 6

GENERAL DISCUSSION

The increasing demand for wheat-based products in Indonesia can be seen by the growth in wheat imports every year, from about 4.5 Mt in 2006 to 5.6 Mt in 2011 (FAO, 2012). Unofficial figures show that in 2012 Indonesia imported about 7 Mt of wheat from countries such as Australia, United States, and Russia (Siregar, 2012). The Indonesian Department of Agriculture targeted commercial production of wheat by 2014 (Medan-Bisnis, 2012; Suhendra, 2012), but this has not been achieved. Production of wheat in a tropical environment presents many challenges and while there are a number of potential limitations to wheat production, a characteristic feature is the constant high temperatures experienced throughout the year which may lead to poor crop establishment, accelerated growth and development, low grain number and yield and also lower grain and dough quality. Therefore, improvement in adaptation of wheat to tropical environments is needed to achieve the goal of commercial wheat production in Indonesia.

This thesis examined the effects of continuously high temperature on the development, growth and the adaptation of wheat to a tropical environment in Indonesia. A series of experiments conducted under controlled environments and in the field on Lombok Island examined particular aspects of adaptation among wheat varieties, which included the responses in development among varieties of different maturities and its impact on yield, the influence of time of sowing on yield and the specific effects of high temperature on the growth and photosynthesis of wheat.

Introduction of wheat production into tropical environments such as Lombok Island needs to consider the environmental limitations and the current farming systems in the area. Weather, including temperature (Slafer and Rawson, 1994; Snape et al., 2001) and rainfall, is among the environmental factors that has a large influence on wheat growth and development on Lombok. The potential growing season of wheat on Lombok is short, like in many low-latitude environments; therefore it is important to develop the most appropriate management practices to match development of the crop to the growing season and allow flowering during the part of the year when temperatures are.

Apart from weather, the growing season is also determined by the characteristics of the farming systems in the region. Lombok's current farming system consists of two rice crops grown during the rainy season and a non-rice crop or fallow during the dry season. Planting the first rice crop starts in September/October when the rainy season begins, followed by a second rice planting season in January/February. The third cropping period in Lombok will suit wheat growing as this is when temperatures are lowest during the year and it coincides with a period of low rainfall. If grown at this time wheat crops would need to be harvested by the end of August or early September to allow the main rice crop to be planted, resulting in an effective growing season of about 3 months.

Lombok is in the tropical zone where temperatures are warm consistently through out the year, but temperature can be modified by elevation, with mean temperature falling by about 0.65°C per 100 m in height. The importance of elevation and lower temperatures to yield was demonstrated in the field trials conducted on Lombok where average grain yields increased by 25g/m^2 per 100 m elevation (Chapter 4), a result that is consistent with other studies in tropical regions but with different rates of increase (Cackett and Wall, 1971; Li et al., 1983; Vega and Vega, 1990; Handoko, 2007). Even though it is not feasible to grow wheat on lowland areas of Lombok consistently because of the low yields, field experiments over two years (2010 and 2011) on Lombok have demonstrated that growing wheat at elevations above 500 m asl can give a reliable yield but success depends on selection of appropriate maturity types and sowing time. Grain yields on Lombok were comparable to those from an earlier study on Java Island-Indonesia in which yields of 2.5 t/ha and 3.3 t/ha were obtained at 500 and 1000 masl on Lombok compared to 1.0 t/ha and

2.7 t/ha at about the same elevation on Java (Handoko, 2007). The higher yields achieved on Lombok Island are, possibly because of a higher solar radiation in the eastern islands of Indonesia (Morrison and Sudjito, 1992).

Given the short dry season on Lombok, the time when wheat is grown will be very important to achieve optimal production on Lombok, and therefore sowing time and maturity type are likely to be crucial in this respect. Sowing can occur from May to early June to allow good crop establishment, flowering when temperatures are low and harvesting before the onset of the rainy season. Sowing earlier, immediately at the end of the rainy season in mid April to early May, when rainfall can still be high increases the risk of poor seed germination and crop establishment, as occurred with the early sowings in 2010. On the other hand, sowing late in mid to late June will expose the crop to rain and rising temperatures at the end of growing period which may cause low yield and poor quality grain from the effects of disease and sprouting grain in the field as the rainy season commences.

Sowing between May and early June contradicts the recommendation on sowing time based on modelling (Handoko, 2007) which showed that the recomended sowing time for wheat on Lombok is from November to February. In fact, these months are the wettest months during the year which will cause severe problems with crop establishment, occurance of diseases especially Fusarium head blight (FHB) and sprouting grain before harvesting. Moreover, sowing during this time with the hottest temperature at the year will affect plant growth, including flowering time which is a sensitive stage to heat stress.

Within the sowing window on Lombok, the optimum sowing time varied with altitude. At low land sites, yields were poorest with the earliest sowing dates and the highest yield were achieved when sowing occurred from the end of May to the end of June. The poor yields from early sowings were likely to be due to poor establishment from waterlogging because sowing occurred at the end of the rainy season and high rainfall occurred and the experiments were sown into rice paddies where soil structure was poor. At the higher altitudes the highest yield were achieved when wheat was sown between mid-May to mid- June. Sowing from mid-May to mid-June at higher elevation caused crops to flower between late July and early August which corresponded to the time when temperatures and rainfall were lowest and solar radiation was increasing. Sowing 2 weeks earlier or later than the optimum time produced a lower yield.

The optimum temperature for early development of wheat (double ridge and terminal spikelet initiation) is around 20°C (Slafer and Rawson, 1995), while on Lombok temperatures exceed this, even at the higher elevations, and these high temperatures delayed DR and TSI. Meanwhile, the response in flowering time differed from that observed with DR and TSI: time to flower is progressively shorter with higher temperatures in all varieties up to 32/23°C. It has been shown by Slafer and Rawson (1994) that the optimum temperature for development increases with later growth stages and the fact that time to flower is not delayed at the highest temperature is consistent with a higher optimum temperature for development after the DR stage. High temperatures reduced time to anthesis and this reduction was related to yield reduction within each variety. Moreover, reduction of time between TSI and anthesis was also correlated with reduction on yield (Chapter 5). The results from the field experiments confirmed that this pre-anthesis stage is the critical stage of development for yield.

The phase of floret development phase, a period of several weeks before anthesis, is especially important to yield (Fischer and Maurer O, 1976), and high temperature during this period reduces the number of grains produced which in turn reduces yield (Shpiler and Blum, 1986; Wheeler et al., 1996; Ferris et al., 1998). It is clear from the growth chamber experiments that higher temperature reduced the time between TSI and anthesis and reduced grain number. A shorter duration of this phase could limit the number of spikelets as well as seed formed (Rawson, 1970; Johnson and Kanemasu, 1983). This effect is also apparent from the field experiment at early sowing times at the lowland site (higher temperature) when the time between DR to anthesis become shorter and this was associated with low grain number, which resulted in low grain yield, although the magnitude of the effect differed among varieties (Chapter 4). Field experiments over 2 years in Lombok have shown that midseason varieties had a longer period between DR and anthesis and this was associated with higher grain yields. Therefore, extending the period of ear development, including time from DR or TSI to anthesis could be used to increase yield at higher temperatures, and is consistent with the importance of grain number in affecting yield (Shpiler and Blum, 1986; Wheeler et al., 1996; Ferris et al., 1998). It is clearly shown that midseason varieties sown from the second week of May to the first week of June is the best choice for wheat grown in Lombok: this strategy had the highest yield which was associated with high grain number.

There was evidence that different maturity types of cultivar have different responses to elevation in Lombok. Mid-season varieties, that flowered after about 60 days in this environment, have higher yield at sites 500 m asl or above compared to lower altitudes. As high elevation should be the target of wheat development on Lombok, midseason varieties that flower after about 60 days should be developed in the future. Early maturing varieties may not be beneficial unless they show a high level of heat tolerance. The heat escape mechanism associated with early flowering cultivars which may be useful in Mediterranean environments is not suitable for tropical environment where heat stress is more persistent during the growing season. As well, the early season varieties like Axe developed very quickly, produced few ears and had low biomass production all of which limited their yield potential in this environment. In contrast, the late maturing varieties produced the lowest yield which was associated with poor grain set and grain growth caused by a high exposure to higher temperature during flowering and grain filling

From the field experiments, varieties with the winter *Vrn* allele were found to be more sensitive to flowering, by delayed time to DR (*Vrn B1-v*) or delayed flowering (*Vrn A1-v and Vrn B1-v*). However, sensitivity to vernalisation in determining flowering were less important than photoperiod genes. Varieties with *PpD1-b* allele which is sensitive to photoperiod showed greater sensitivity to temperature in time to flower. Therefore, varieties with the insensitive allele (*PpD1-a*) were more suitable to be adapted on Lombok Island. That midseason varieties perform the best in this experiment could be caused by photoperiod control mechanism since most of them possesses the *PpD1-a* allele except Gladius which has sensitivity to photoperiod.

High temperatures are a pervasive feature of tropical environments, and even though the effect could be alleviated by growing wheat at higher elevation, heat stress is still an important limitation to achieving high production. In contrast with many other wheat growing regions where high temperatures are more common at particular stages of development, on Lombok high temperatures can occur at all stages of growth. The specific effects of these continuous high temperatures on growth and yield were examined under controlled conditions to understand better their influence on yield where two temperature treatments, 30/23°C and 28/20°C, were selected to simulate lowland and upland sites respectively on Lombok. At 30/23°C, rapid development resulted in low biomass production, restricted tillering and low grain set which greatly reduced grain yield compared to wheat grown at 28/20°C. This effect was related to the fact that at high temperature (32/23°C), photosynthesis rate, respiration rate and stomatal conductance are substantially reduced. The growth room experiment showed that there is a big difference on photosynthetic rate,stomatal conduction and respiration rate between 32/23°C and 28/20°C but relatively small difference was found between 28/20°C and 25/15°C and this small difference between 28/20°C and 25/15°C is also strongly related to yield. That is why the temperatures experienced at lowland sites may impose severe limitationson growth and yield. Consequently growing wheat at lowland sites on Lombok consistently is not considered to be feasible because of the high temperatures experienced throughout the life cycle of the crop.

The growth room experiment also demonstrated the importance of WSC to yield at high temperatures. High photosynthetic rates contributed to the accumulation of WSC in stems, and ultimately to grain weight which resulted in higher yield. Remobilisation of WSC is an important trait to maintain the supply of carbon to the grain when the photosynthetic rate has declined (Blum et al., 1994; van Herwaarden et al., 1998; McIntyre et al., 2011) and appears to be an important characteristic for adaptation to high temperatures. There was also a small effect of WSC on grain set and so the ability to accumulate stem WSC may enhance grain set under high temperatures

Genetic variability to response heat stress was evident. The two Indonesian varieties which presumably were developed for a warm climate, were more tolerant to high temperatures than the Australian varieties as seen in higher yield and biomass produced, and this is highly correlated to the ability to maintain a higher rate of photosynthesis and stomatal conductance. Nias especially appeared relatively heat tolerant. Nias was derived from Thailand germplasm (Thai-88) (Human, 2002; Jusuf, 2002) but no further information is available on its pedigree. Dewata was originally derived from Indian germplasm, was released in 1993 as DWR 162 and reccommended for the Peninsula Zone of India (Jain, 1994). After a series of adaptation trials in Indonesia, it was released as Indonesian varieties of Dewata.

Together with Selayar, another Indonesian wheat variety derived from CIMMYT germplasm (Jusuf, 2002), Nias and Dewata are used as control varieties in some recent wheat adaptation trials in Indonesia with introduced varieties from India (in Java, Sulawesi, or Papua) (Rogi and Frans, 2011; Ashari et al., 2012; Wahyu et al., 2013), from Slovakia (in West Sumatera) (Putri et al., 2013) and from Australia (our trials on Lombok), and also some trials of new breeding lines, with conventional breeding or radiation treatment. In these trials, Indonesian varieties do not always yield better than introduced varieties therefore development of higher yielding adapted wheat varieties in Indonesia is still needed. Even though the goal of commercial wheat cropping in 2014 was not accomplished, with more wheat trials recently, commercial wheat cropping in Indonesia will be implemented in near future.

Conclusion

Matching wheat growth with the environment of Lombok is a key factor for success in wheat production. Wheat yield on Lombok shows that higher elevations give a higher yield. Sowing wheat in May-early June at medium to high elevations of Lombok Island is an important part of a potential rice-wheat production system on Lombok. This allows the wheat crop to mature and be harvested in late August or early September before the onset of rainy season and the need for the next crop to be planted. Variety choice is also important, mid season variety will match to the growing period, to flower on the lowest temperature during the year on Lombok. This would allow wheat to fit in with the current cropping systems.

While it was not the focus of the current study, the field trials demonstrated that leaf disease can be a serious problem that will affect yield and grain quality. While the incidence and severity of disease was affected by location and time of sowing, it is an important aspect of wheat production on Lombok.

Future work

Future work should be focussed on adapting wheat varieties into broader areas on Lombok and other regions of Indonesia by breeding for improved stress tolerance and diseses resistance and improving yield by developing appropriate cropping practices. This may also include breeding and adapting new introduced heat stress or ather biotic and abiotic stress resistant varieties.

(i) *Adapting wheat varieties into broader areas available in Indonesia.* Although the Indonesia archipelago straddles the equator and has a relatively constant temperature, Lombok is a bit different to other parts of Indonesia in terms in terms of the amount of solar radiation, the mean temperatures received during the cooler months and the length of the rainy season, as well as the soil properties. Therefore, experiments on wheat adaptation should be done in other parts of Indonesia. Different genotypes will need to be tested over a range of different environmental conditions to characterise differences in crop development, biomass production and yield.

(ii) *Improving yield by appropriate cropping practises.* Crop management practices such as optimal time for planting, plant density, irrigation and fertilization will be critical in sustaining wheat yields in warm environments. These cropping practices need to be adjusted for areas with different altitude and yield potential. Therefore a series of regional agronomic trials examining the effects of variety, sowing time, plant density and nutrition should be established. These should include studies that examine the interactions between important agronomic inputs. A focus of these trials should include the management of disease for yield and grain quality. As well as being used to establish appropriate management practices for different environments on Lombok Island, these trials could also involve farmers and serve as an education and extension exercise to introduce a new crop to the island's farmers.

(iii) *Breeding varieties for improved heat stress and resistance/tolerance to other biotic and abiotic stresses.* Genetic variability is an important factor in wheat breeding programs therefore by increasing genetic variability by hybridization of varieties or lines with various important characters as well as various agronomic characters important for higher yield would help wheat development in Indonesia. The key traits that need to be considered are tolerance to high temperatures, improved disease and insect resistance, as well as waterlogging tolerance for areas prone to waterlogging during establishment.

References:

Ashari, S., Waluyo, B., Yulianah, I., Kendarini, N., Jusuf, M., 2012. Stability of wheat genotypes adapted in tropical medium and lowland. Agrivita 34, 1-9.

Blum, A., Sinmena, B., Mayer, J., Golan, G., Shpiler, L., 1994. Stem Reserve Mobilisation Supports Wheat-Grain Filling Under Heat Stress. Australian Journal of Plant Physiology 21, 771-781.

Cackett, K.E., Wall, P.C., 1971. The effect of altitude and season length on the growth and yield of wheat (Triticum aestivum L.) in Rhodesia. Rhodesian Journal of Agricultural Research 9, 107-120.

FAO, 2012. FAO Statistics (http://www.fao.org/crop/statistics/en/). Food and Agriculture Organisation of The United Nations, Rome, Italy.

Ferris, R., Ellis, R.H., Wheeler, T.R., Hadley, P., 1998. Effect of High Temperature Stress at Anthesis on Grain Yield and Biomass of Field-grown Crops of Wheat. Annals of Botany 82, 631-639.

Fischer, R.A., Maurer O, R., 1976. Crop temperature modification and yield potential in a dwarf spring wheat. Crop Science 16, 855-859.

Handoko, I., 2007. Gandum 2000: Penelitian pengenbangan gandum di Indonesia (Wheat 2000: Wheat research and development in Indonesia). SEAMEO_BIOTROP, Jakarta.

Human, S., 2002. Riset dan pengembangan sorgum dan gandum untuk ketahanan pangan (Research and development of Shorgum and Wheat for Food Security). Pertemuan Koordinasi Penelitian dan Pengembangan. Gandum (Coordination Meeting on Wheat Development in Indonesia). Department of Agriculture, Jakarta.

Jain, K.B.L., 1994. Wheat cultivars in India; Names, pedigree, origins and adaptations. Directorat of Wheat Research, Kamal, Haryana - India.

Johnson, R.C., Kanemasu, E.T., 1983. Yield and Development of Winter Wheat at Elevated Temperatures. Agron. J. 75, 561-565.

Jusuf, M., 2002. Hasil-hasil penelitian budidaya gandum dan strategi pengembangannya di masa datang (Research on wheat cropping and development strategic in the future). Pertemuan Koordinasi Penelitian dan Pengembangan Gandum (Coordination Meeting on Wheat Development in Indonesia). Department of Agriculture, Jakarta.

Li, C., Zhang, H., Lin, D., 1983. Response of winter wheat Triticum sativum cultivar Fengmai-13 to the climate at different altitudes. 2. Accumulation and partitioning of dry matter of aerial part. Acta Botanica Yunnanica 5, 301-304.

McIntyre, C.L., Casu, R.E., Rattey, A., Dreccer, M.F., Kam, J.W., van Herwaarden, A.F., Shorter, R., Xue, G.P., 2011. Linked gene networks involved in nitrogen and carbon metabolism and levels of water-soluble carbohydrate accumulation in wheat stems. Functional & Integrative Genomics 11, 585-597.

Medan-Bisnis, 2012. Kementan: Budidaya gandum meluas dilakukan mulai 2014 (Indonesian Dept. Agric.: Growing wheat commecially will be starting at 2014). Medan Bisnis, Medan.

Morrison, G.L., Sudjito, 1992. Solar radiation data for Indonesia. Solar Energy 49, 65-76.

Putri, N.E., Chaniago, I., Suliansyah, I., 2013. Seleksi beberapa genotype gandum berdasarkan komponen hasil di daerah curah hujan tinggi (Selection to Several Wheat Genotypes based on yield component in a high rainfall area). Jurnal Agroteknologi 4, 1-6.

Rawson, H., 1970. Spikelet Number, Its Control and Relation to Yield Per Ear in Wheat. Australian Journal of Biological Sciences 23, 1-16.

Rogi, J.E.X., Frans, S.J., 2011. Predicting potency wheat (Triticum aestivum) production in North Sulawesi using Shierary Wheat ver. 2.2. Eugenia 17, 60-70.

Shpiler, L., Blum, A., 1986. Differential reaction of wheat cultivars to hot environments. Euphytica 35, 483-492.

Siregar, S., 2012. Import gandum diperkirakan capai 7.4 juta ton. Indonesia Finance Today. Indonesia Finanindo Media, Jakarta.

Slafer, G.A., Rawson, H.M., 1994. Sensitivity of wheat phasic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. Australian Journal of Plant Physiology 21, 393-426.

Slafer, G.A., Rawson, H.M., 1995. Rates and cardinal temperatures for processes of development in wheat: effects of temperature and thermal amplitude. Aust. J. Plant Physiol 22, 913-926.

Snape, J.W., Butterworth, K., Whitechurch, E., Worland, A.J., 2001. Waiting for fine times: genetics of flowering time in wheat. Euphytica 119, 185-190.

Suhendra, 2012. Kurangi Impor, RI Produksi Gandum Secara Massal Mulai 2014. Detik Finance. Detikcom, Jakarta.

van Herwaarden, A.F., Angus, J.F., Richards, R.A., Farquhar, G.D., 1998. 'Haying-off', the negative grain yield response of dryland wheat to nitrogen fertiliser - II. Carbohydrate and protein dynamics. Australian Journal of Agricultural Research 49, 1083-1093.

Vega, O.U.A., Vega, J.A., 1990. Response of wheat and triticale varieties to different altitudes in Venezuela. Revista de la Facultad de Agronomia, Universidad Central de Venezuela 16, 13-26.

Wahyu, Y., Samosir, A.P., Budiarti, S.G., 2013. Adaptabilitas Genotipe Gandum Introduksi di Dataran Rendah (Adaptability of Introduced Wheat Genotypes at Low Altitude). Bul. Agrohorti 1, 1-6.

Wheeler, T.R., Hong, H.D., Ellis, R.H., Batts, G.R., Morison, J.I.L., Hadley, P., 1996. The duration and rate of grain growth, and harvest index, of wheat (Triticum aestivum L) in response to temperature and CO2. Journal of Experimental Botany 47, 623-630.

CHAPTER 7

SUPPLEMENTARY TABLES AND FIGURES

Supplementary Table 3.1 Average yield and yield components of crops at different time of sowing in Experiment 2010.

TOS	Yield (g m^{-2})	DM (g m^{-2})	Ears m^{-2}	Spikelet /head	Grain/ m^2	Grains /spikelet	HI (%)	TGW (g)
				Gunung Sari				
19-Apr	20	153	193	9.3	962	0.5	13.5	20.1
3-May	38	247	283	11.2	1535	0.5	14.5	23.2
17-May	47	275	328	11.0	1913	0.6	16.2	24.0
31-May	61	317	320	11.5	2740	0.7	19.0	22.7
15-Jun	59	282	328	10.8	2979	0.9	21.0	20.6
28-Jun	65	318	391	10.8	3487	0.8	19.7	18.7
LSD	9.6	29.7	39.9	0.5	444.1	0.1	2.43	1.52
				Narmada				
29-May	78	268	259	11.0	3512	1.3	28.7	21.5
12-Jun	83	328	337	10.9	4287	1.3	27.2	20.4
26-Jun	72	279	318	10.3	3716	1.2	27.1	19.0
LSD	ns	38.3	35.8	ns	618.0	ns	ns	1.87
				Sembalun				
18-Apr	337	971	551	12.2	12059	1.8	35.5	27.8
2-May	367	979	492	13.2	12396	2.0	37.6	29.4
16-May	371	914	455	12.8	11602	2.1	40.4	31.8
30-May	318	747	432	12.2	10109	2.1	42.9	31.8
13-Jun	326	843	584	11.1	12732	2.1	39.4	25.5
27-Jun	220	635	528	11.5	8825	1.8	35.2	25.4
LSD	32.7	78.2	41.8	0.66	1047	0.09	1.99	1.31

Supplementary Table 3.2. Average yield and yield components of four varieties of bread wheat sown at three locations on Lombok Island in 2011.

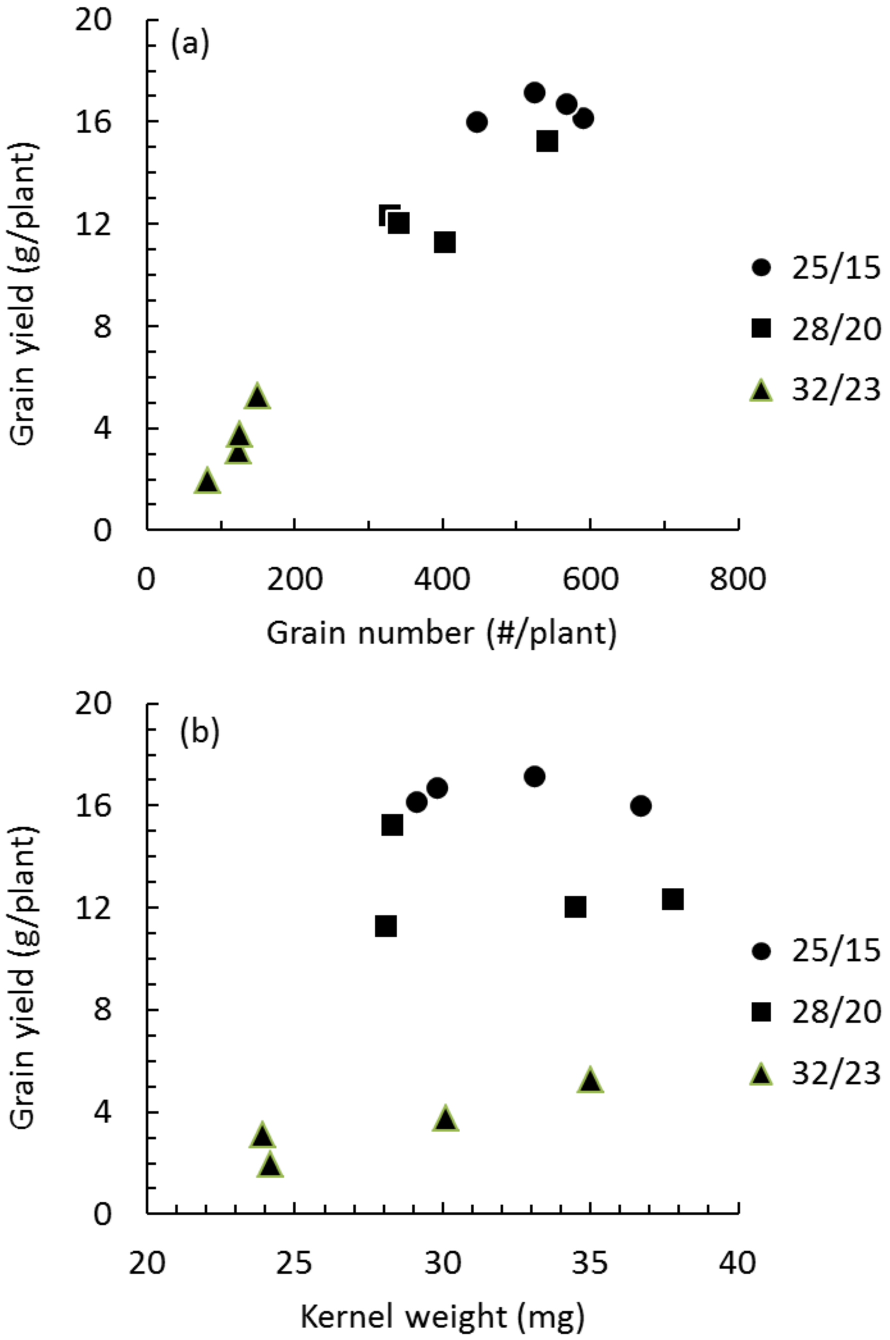
		Site		Mean
Sowing date	Lekok	Senaru	Sembalun	
		Grain yield (g m^{-2})		
Axe	102	196	350	216
Gladius	118	234	261	204
Nias	133	207	334	224
Dewata	118	259	323	233
Mean	117	224	317	
LSD		Site 45; Sowing time 45		
		Site x Sowing time (a) 47; (b) 60		
		Total dry weight (g m^{-2})		
Axe	303	402	849	511
Gladius	409	661	673	581
Nias	454	588	862	635
Dewata	531	803	909	748
Mean	424	613	818	
LSD		Site 108; Sowing time 108		
		Site x Sowing time (a) 139; (b) 159		
		Grains m^{-2}		
Axe	4642	5985	11882	7503
Gladius	4334	8366	9135	7278
Nias	6746	8688	11632	9022
Dewata	5900	9558	11644	9034
Mean	5406	8149	11073	
LSD		Site 1316; Sowing time 1316		
		Site x Sowing time (a) 1944; (b) 2106		
		Thousand grain wt (g)		
Axe	27.0	38.1	31.4	32.2
Gladius	32.1	32.4	37.2	33.9
Nias	29.1	36.1	32.8	32.7
Dewata	28.9	36.2	36.2	33.8
Mean	29.2	34.4	35.7	
LSD		Site 1.61; Sowing time 1.61		
		Site x Sowing time (a) 2.27; (b) 2.51		

[A] Range of sowing times among the three sites; [B] LSD (a) Comparisons within site; (b) other comparisons

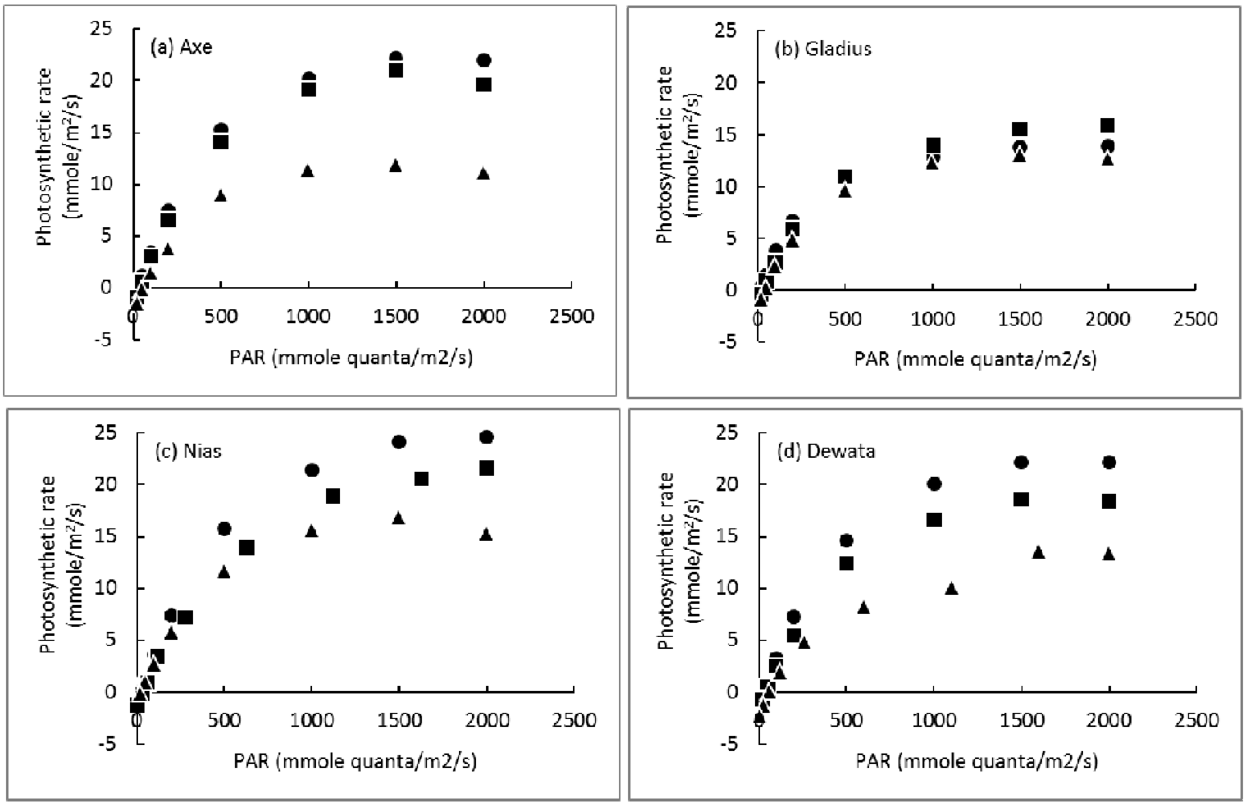
Supplementary Table 4.1. Comparisons of ANOVA of the time of sowing experiments at three sites on Lombok based on fully replicated randomised complete block design or treating the experiment as unreplicated and using sowing times and varieties as pseudoreplicates to test the effects of Variety and Sowing date respectively.

Fully replicated			Based on pseudoreplicates		
Source	GY		Source	GY	TDM
Sembalun					
Sowing date	ns	ns	Sowing date	ns	ns
Variety	P=0.05	ns	Variety	P=0.083	ns
SDxVar	ns	ns			
Lekok					
Sowing date	P<0.001	P<0.001	Sowing date	P<0.001	P<0.001
Variety	P=0.01	P=0.003	Variety	P=0.013	P<0.001
SDxVar	P=0.018	ns			
Senaru					
Sowing date	P<0.001	P=0.003	Sowing date	P<0.001	P<0.001
Variety	P<0.001	P<0.001	Variety	P<0.001	P<0.001
SDxVar	P<0.001	P<0.001			

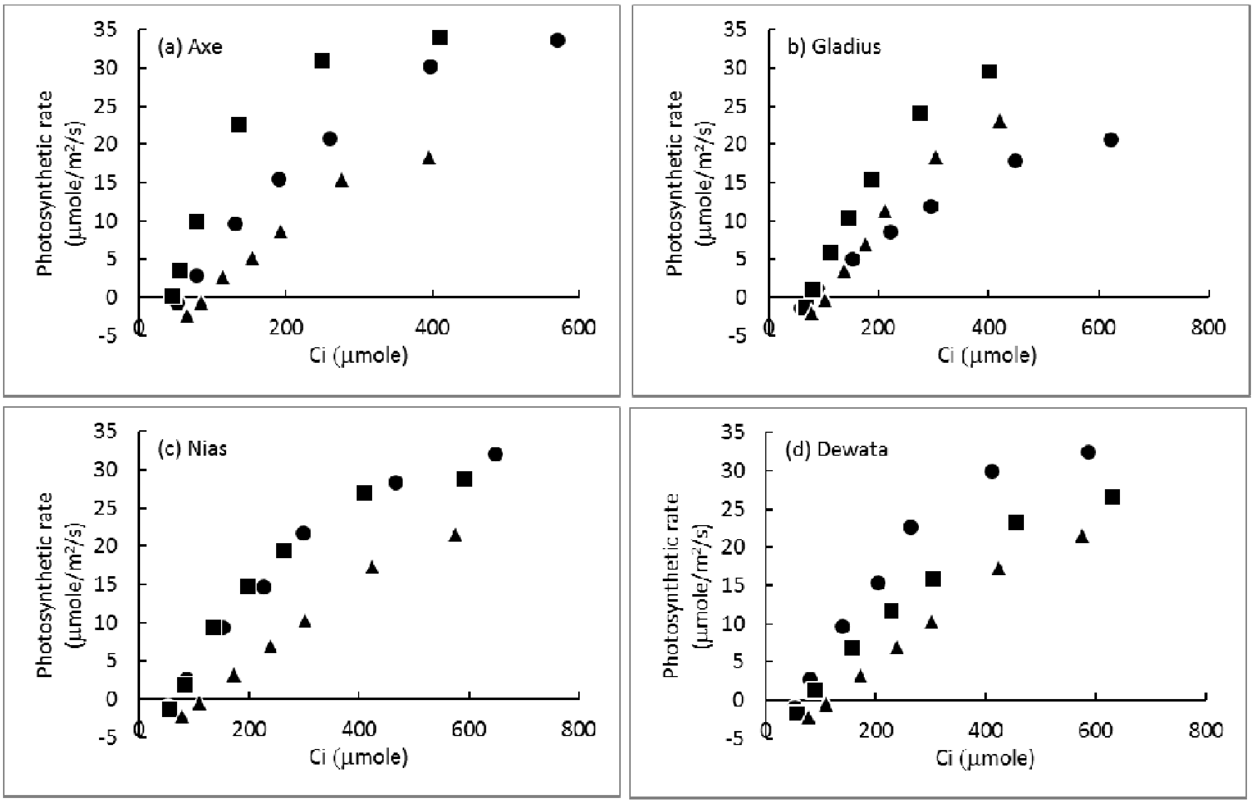
Supplementary figures



Supplementary Fig.5.1. The relationships between grain yield per plant and (a) grain number per plant and (b) kernel weight for four varieties of wheat grown at three temperatures



Supplementary Figure 5.2. The light response curves for four wheat varieties grown at 25°/15°C (●). 28°/20°C (■) or 32°/32°C (▲)



Supplementary Figure 5. 3. The CO_2 response curves for four wheat varieties grown at 25°/15°C (●). 28°/20°C (■) or 32°/32°C (▲)